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Phylogenetic delimitation of *Apiospora* and *Arthrinium*

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Abstract: In the present study six species of *Arthrinium* (including a new taxon, *Ar. crenatum*) are described and subjected to phylogenetic analysis. The analysis of ITS and 28S rDNA, as well as sequences of *tef1* and *tub2* exons suggests that *Arthrinium s. str.* and *Apiospora* represent independent lineages within *Apiosporaceae*. Morphologically, *Arthrinium* and *Apiospora* do not seem to have clear diagnostic features, although species of *Arthrinium* often produce variously shaped conidia (navicular, fusoid, curved, polygonal, rounded), while most species of *Apiospora* have rounded (face view) / lenticular (side view) conidia. Ecologically, most sequenced collections of *Arthrinium* were found on *Cyperaceae* or *Juncaceae* in temperate, cold or alpine habitats, while those of *Apiospora* were collected mainly on *Poaceae* (but also many other plant host families) in a wide range of habitats, including tropical and subtropical regions. A lectotype for *Sphaeria apiospora* (syn.: *Ap. montagnei*, type species of *Apiospora*) is selected among the original collections preserved at the PC fungarium, and the putative identity of this taxon, found on *Poaceae* in Mediterranean lowland habitats, is discussed. Fifty-five species of *Arthrinium* are combined to *Apiospora*, and a key to species of *Arthrinium s. str.* is provided.

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INTRODUCTION

The genus *Arthrinium* was proposed by Kunze & Schmidt (1817) and validated by Fries (1832) for *Ar. caricicola*, a species found on *Carex* (*Cyperaceae*) in Berlin (Germany) for which a lectotype (BPI 422608) and an epitype (CBS H-24083) were recently designated by Crous *et al.* (2020). Several other species of *Arthrinium* were found later in temperate, cold or alpine regions, mainly growing on *Cyperaceae* and *Juncaceae* hosts, but also *Poaceae* (Table 1). Most taxa were subsequently recollected, allowing researchers to confirm their distinct identity (Cooke 1954, Gjørnum 1966, Scheuer 1996, Minter & Cannon 2018). Some of these species were relocated to different genera by Link (in Willdenow 1824) because of their different conidial shape, *e.g.*, *Camptoum* (type species *C. curvatum* ≡ *Ar. curvatum*), *Gonatosporium* (type species *G. puccinioides* ≡ *Ar. puccinioides*), *Goniosporium* (type species *G. puccinioides* ≡ *Ar. puccinioides*), *Sporophleum* (type species *S. gramineum* = *Ar. sporophleum*). However, they were later again reduced to synonymy with *Arthrinium* because of their similar conidiophores and conidiogenesis (von Höhnel 1925, Cooke 1954). The type species of *Turenia*, *T. juncoidea*, is considered a heterotypic synonym of *Ar. cuspidatum*, and therefore, *Turenia* was also synonymized with *Arthrinium* (Cooke 1954).

Another large group of *Arthrinium* spp. occurs in a wide variety of climates (including tropical and subtropical regions) in association with *Poaceae*, as well as many other host plant families (including *Cyperaceae* and *Juncaceae*). The first species

to be described in this group was probably *Ar. saccharicola* (Johnston & Stevenson 1917), which was found growing on *Saccharum officinarum* (*Poaceae*) in the coastal lowlands of Puerto Rico. Later, Subramanian (1956) combined another asexual species found on *Saccharum officinarum*, *Microtypha saccharicola* (type species of *Microtypha*), into *Arthrinium*, renaming it as *Ar. spegazzinii*. Ellis (1965) synonymized several other asexual genera with basauxic conidiogenesis under *Arthrinium* (Hughes 1953, Cole & Samson 1979, Minter 1985). One such genus, *Papularia* Fr. (actually an illegitimate name, *non Papularia* Forssk.), was considered the asexual morph of *Apiospora* (Saccardo 1875) by von Höhnel (1919), Petrak (1925) and Hudson (1960, 1963a). As a result, a biological relationship between *Arthrinium* and *Apiospora* was widely accepted after Ellis (1965). Other asexual genera synonymized with *Arthrinium* by Ellis (1965) included *Innatospora* (type species, *I. rosea* = *Ar. arundinis sensu* Ellis) and *Pseudobasidium* (type species *P. bicolor* = *Ar. phaeospermum sensu* Ellis). Samuels *et al.* (1981), showed a biological relationship between *Apiospora* and species of asexual genera such as *Cordella* (type species *Cordella spinulosa*), *Pteronidium* (type species *P. asteroides* = *Ar. pterospermum sensu* von Arx 1981), and *Scyphospora* (type species *S. phyllostachydis* = *Ar. hysterinum*, Sivanesan 1983, Kirk 1986), and hence these taxa were also considered as synonyms of *Arthrinium*. Due to these synonymies, multiple species occurring on European canes (*Arundo*, *Phragmites* — *Poaceae*) and Asian bamboo (*Bambusa*, *Phyllostachys* — *Poaceae*) were combined into *Arthrinium* (*e.g.* *Ar. arundinis*, Dyko & Sutton

Table 1. Species of *Arthrinium s. str.* with the references containing the protologues, as well as the hosts and regions mentioned in the protologues.

Species	References	Host	Region
<i>Ar. austriacum</i>	Petrak (1959)	<i>Carex</i> (Cyperaceae)	Wienerwald, Austria
<i>Ar. bicorne</i>	Rostrup (1886)	<i>Juncus</i> (Juncaceae)	Kaafjord, Norway
<i>Ar. caricicola</i>	Kunze & Schmidt (1817)	<i>Carex</i> (Cyperaceae)	Berlin, Germany
<i>Ar. carinatum</i>	Bucholtz (1916)	<i>Carex</i> (Cyperaceae)	Saaremaa, Estonia
<i>Ar. crenatum</i>	Present study	(Poaceae), <i>Carex</i> (Cyperaceae)	Côte-d'Or, France
<i>Ar. curvatum</i>	Kunze & Schmidt (1823)	<i>Scirpus</i> (Cyperaceae)	Leipzig, Germany
<i>Ar. cuspidatum</i>	Cooke (1883), Tranzschel (1914)	<i>Scirpus</i> (Cyperaceae)	Mount Shasta, California, USA
<i>Ar. fuckelii</i>	Gjærum (1967)	<i>Carex</i> (Cyperaceae)	Norway
<i>Ar. globosum</i>	Koskela (1983)	<i>Carex</i> (Cyperaceae)	Oulu, Finland
<i>Ar. japonicum</i>	Pollack & Benjamin (1969), Yokoyama & Benjamin (1979)	<i>Carex</i> (Cyperaceae)	Aomori, Japan
<i>Ar. juncoideum</i>	Hall (1915), Saccardo (1931)	<i>Juncus</i> (Juncaceae)	Washington, USA
<i>Ar. kamtschaticum</i>	Elenkin (1914), Pollack & Benjamin (1969)	<i>Carex</i> (Cyperaceae)	Kamtchatka, Russia
<i>Ar. lobatum</i>	Ellis (1963)	(Poaceae)	Mucubají, Venezuela
<i>Ar. luzulae</i>	Ellis (1965)	<i>Luzula</i> (Juncaceae)	Switzerland
<i>Ar. morthieri</i>	Fuckel (1870)	<i>Carex</i> (Cyperaceae)	Dombresson, Switzerland
<i>Ar. muelleri</i>	Ellis (1976)	<i>Carex</i> (Cyperaceae)	Switzerland
<i>Ar. naviculare</i>	Rostrup (1886)	<i>Carex</i> (Cyperaceae)	Vasbottenfjaeld, Norway
<i>Ar. puccinioides</i>	Kunze & Schmidt (1823)	<i>Carex</i> (Cyperaceae)	Léman, France
<i>Ar. sphaerospermum</i>	Fuckel (1874)	<i>Phleum</i> (Poaceae)	Jura, France
<i>Ar. sporophleoides</i>	Fuckel (1874)	<i>Carex</i> (Cyperaceae)	Budenheim, Germany
<i>Ar. sporophleum</i>	Kunze & Schmidt (1823)	(Poaceae)	Grenznach, Germany
<i>Ar. ushuvaiense</i>	Speggazzini (1887)	<i>Luzula</i> (Juncaceae)	Tierra del Fuego, Argentina

1979), synonymized with other species of this genus (e.g. *P. sphaerosperma* (Pers.) Höhn = *Ar. phaeospermum sensu* Ellis 1965), or proposed as new (e.g. *Ar. macrosporum*, Liu *et al.* 1976).

More recently, with the aid of genetic data, *Apiospora* and *Arthrinium* were placed in their own family *Apiosporaceae* (Hyde *et al.* 1998), and finally, Crous & Groenewald (2013) synonymized them (with *Arthrinium* having priority) on the basis of the one fungus- one name policy (Hawksworth *et al.* 2011). Crous & Groenewald (2013) also resolved the genetic identity of multiple species of *Arthrinium* (= *Apiospora*), analysing ex-type collections, and confirmed that most species occur in *Poaceae* hosts, although some were known from *Amaranthaceae*, *Cyperaceae*, *Euphorbiaceae*, *Fagaceae*, *Juncaceae*, *Restionaceae*, *Vitaceae* and even seaweeds. Later, Wang *et al.* (2018) provided genetic evidence of *Arthrinium* (= *Apiospora*) records on *Theaceae* and *Rosaceae*, but observed that two species occurring on *Carex* spp. (*Ar. japonicum* and *Ar. puccinioides*, sequences produced by Goto *et al.* unpubl. data) formed a monophyletic clade apparently unrelated with the remaining taxa. Pintos *et al.* (2019) published the first genetic data from the type species of *Arthrinium*, *Ar. caricicola*, and samples occurring on *Carex* and *Juncus*, identified by them as *Ar. curvatum* and *Ar. sporophleum*. These samples form a monophyletic clade with those identified as *Ar. japonicum* and *Ar. puccinioides*, distinct from all other sequences of *Arthrinium* (= *Apiospora*). The authors suggested that *Arthrinium s. str.* could actually be phylogenetically different from *Apiospora*, but considered that confirming the phylogeny of additional species was necessary before making a taxonomic decision on the issue.

In the present work, this task is accomplished. The taxonomic status of the lineage including *Ar. caricicola* is re-examined after producing genetic data from additional taxa occurring on *Cyperaceae* and *Juncaceae* occurring in temperate or cold regions. A lectotype for *S. apiospora* (\equiv *Ap. montagnei*) is selected to fix the ecological concept of this species and its clade, while the taxonomic status of *Arthrinium* species is updated in accordance with the phylogenetic results obtained.

MATERIALS AND METHODS

Samples studied

To isolate sexual morphs, fresh mature ascomata were soaked in water for 2 h, and then placed in the base of a Petri-dish lid and covered with the inverted base containing 2 % water agar (WA) culture medium supplemented with 500 mg/L chloramphenicol. Inverted plates were incubated at room temperature for 24 h. Germinated ascospores in the culture medium were transferred to 2 % malt extract agar (MEA) plates (e.g. Crous *et al.* 2019), which were incubated at room temperature. To isolate asexual morphs, conidia from colonies growing on the host were sampled with a sterilized needle and streaked over the surface of a Petri dish containing 2 % WA supplemented with 200 mg/L penicillin. The germinated conidia were then transferred to 2 % MEA plates and incubated at room temperature.

In addition to cultures obtained from fresh collections, several fungarium samples were retrieved from the public fungaria such as Cornell University (CUP, Ithaca, USA), Karl-

Franzens-Universität Graz (GZU, Graz, Austria), Martin-Luther-Universität (HAL, Halle, Germany), and Muséum National d'Histoire Naturelle (PC, Paris, France), as well as several private collections from Alain Gardiennet (AG), Ángel Pintos (AP), Edwin W. Johanssen (EWJ), and Volker Kummer (VK). Images and data from type specimens were also retrieved from the Farlow Fungarium (FH, Harvard University, USA), as well as the Conservatory and Botanical Garden of the City of Geneva (G, Geneva, Switzerland). Cultures were deposited at Westerdijk Fungal Biodiversity Institute (CBS, Utrecht, The Netherlands).

DNA isolation, amplification and phylogeny

Total DNA was extracted from cultured isolates and dried fungarium specimens employing a modified protocol based on Murray & Thompson (1980). Amplification reactions (Mullis & Faloona 1987) included 35 cycles with an annealing temperature of 54 °C. Primers ITS1F and ITS4 (White *et al.* 1990, Gardes & Bruns 1993) were employed to amplify the ITS1-5.8S-ITS2 nrDNA region (ITS), while LR0R and LR5 (Vilgalys & Hester 1990, Cubeta *et al.* 1991) were used for the 28S nrDNA region (LSU), EF1-728F, EF1-983F and EF1-1567R (Carbone & Kohn 1999, Rehner & Buckley 2005) for the translation elongation factor 1- α (*tef1*) gene, and T1, Bt2a, and Bt2b (Glass & Donaldson 1995; O'Donnell & Cigelnik 1997) for the β -tubulin gene (*tub2*). PCR products were checked in 1% agarose gels, and positive reactions were sequenced with one or both PCR primers. Chromatograms were checked searching for putative reading errors in MEGA v. 5.0 (Tamura *et al.* 2011), and these were corrected.

Two different sequence alignments were built (Table 2): 1) an alignment of 5.8S-ITS2 nrDNA, 28S nrDNA, as well as the *tef1* exon between introns 1 and 2 (Stielow *et al.* 2015), and the *tub2* exon between introns 4 and 5, plus the 5' region of

the exon between introns 5 and 6, obtained from selected samples of *Apiosporaceae* and other related families of order *Amphisphaeriales* (using *Triangularia verruculosa* from order *Sordariales* as outgroup), and 2) an alignment of ITS1-5.8S-ITS2 nrDNA, 28S nrDNA, as well as 5' extreme of the *tef1* exon between introns 2 and 3, and *tub2* introns 3–5 with the exons between them plus the 5' extreme of the exon between introns 5 and 6, obtained from all samples of *Arthrinium s. str.* available in public databases (using *Ap. tintinnabula* ex-type as outgroup). BLAST (Altschul *et al.* 1990) was used to select the most closely related sequences from the International Nucleotide Sequence Database Collaboration (INSDC, Cochrane *et al.* 2011) public database, and UNITE (Nilsson *et al.* 2018). The sequences employed (Supplementary Table S1) were mainly retrieved from Smith *et al.* (2003), Singh *et al.* (2012), Crous & Groenewald (2013), Crous *et al.* (2015, 2020), Senanayake *et al.* (2015), Dai *et al.* (2016, 2017), Wang *et al.* (2017, 2018), Jiang *et al.* (2018, 2019, 2020), Liu *et al.* (2019), Pintos *et al.* (2019), Yan *et al.* (2019), and Yang *et al.* (2019). Sequences first were aligned in MEGA software with its Clustal W application and then corrected manually. The number of sequences from each locus, as well as total sites and variable sites analyzed are reported in Table 2. ITS data were subjected to GBlocks v. 0.91b (Castresana 2000) to remove 71 ambiguously aligned positions from the alignment of *Amphisphaeriales*.

The aligned loci were loaded in PAUP v. 4.0b10 (Swofford 2003) and each partition was subjected to MrModeltest v. 2.3 (Nylander 2004) to select the best fitting evolutionary model for each partition (Table 2). GTR+G+I was selected for 5.8S-ITS2, LSU and *tub2* introns, GTR+G for the 3rd codon positions of *tef1* and *tub2* exons, JC for *tef1* 1st and 2nd positions, and JC+G for *tub2* exon 1st and 2nd positions. The concatenated dataset of each analysis was loaded in MrBayes v. 3.2.6 (Ronquist *et al.*

Table 2. Partitions employed for phylogenetic analyses with the best fitting evolutionary model for each partition, as well as the number of variable sites, total sites and sequences analysed of each marker.

Partition	Model	Variable sites	Total sites	Sequences
<i>Amphisphaeriales</i>	–	541	1429	–
5.8S-ITS2 rDNA	GTR+G+I	132	281	149
28S rDNA	GTR+G+I	270	801	138
<i>tef1</i> — exon between introns 1–2 /1st codon position	JC	58	138	91
<i>tef1</i> — exon between introns 1–2 /2nd codon position	JC	58	138	91
<i>tef1</i> — exon between introns 1–2 /3rd codon position	GTR+G	58	138	91
<i>tub2</i> — 5' of exons between introns 4–5 and 5–6 /1st codon position	JC+G	81	209	102
<i>tub2</i> — 5' of exons between introns 4–5 and 5–6 /2nd codon position	JC+G	81	209	102
<i>tub2</i> — 5' of exons between introns 4–5 and 5–6 /3rd codon position	GTR+G	81	209	102
<i>Arthrinium s. str.</i>	–	747	2436	–
ITS1-5.8S-ITS2 rDNA	GTR+G+I	157	477	44
28S rDNA	GTR+G+I	64	797	20
<i>tef1</i> — 5' of exon between introns 2–3 /1st codon position	JC	69	393	11
<i>tef1</i> — 5' of exon between introns 2–3 /2nd codon position	JC	69	393	11
<i>tef1</i> — 5' of exon between introns 2–3 /3rd codon position	GTR+G	69	393	11
<i>tub2</i> — introns 3–5 with intermediate exons	GTR+G+I	424	620	20
<i>tub2</i> — 5' of exon between introns 5–6 /1st codon position	JC+G	33	149	19
<i>tub2</i> — 5' of exon between introns 5–6 /2nd codon position	JC+G	33	149	19
<i>tub2</i> — 5' of exon between introns 5–6 /3rd codon position	GTR+G	33	149	19

2012), where a Bayesian analysis (BA) was performed (data partitioned as reported above with the best fitting model, two simultaneous runs, four chains, temperature set to 0.2, sampling every 100th generation) until convergence parameters were met after 9.05 M (*Amphisphaeriales*) and 1.28 M (*Arthrinium s. str.*) generations, standard deviation having fell below 0.005. RWTY (Warren *et al.* 2017) was employed to estimate sample size (>200 ESS in all analyses), and select the proper burn in (first 2.5 M generations in *Amphisphaeriales* and 0.25 M in *Arthrinium s. str.*). Finally, a full search for the best-scoring maximum likelihood (ML) tree was performed in RAxML v. 8.2.12 (Stamatakis 2014) using the standard search algorithm (data partitioned as for BA, GTRCAT model for *Amphisphaeriales*, GTRGAMMA model for *Arthrinium s. str.*, 2 000 bootstrap replications). Significance threshold was set above 0.95 for posterior probability (PP) and 70 % bootstrap proportions (BP). Separate alignments of 5.8-ITS2, LSU, *tef1* exon and *tub2* exon sequences of *Apiosporaceae* were subjected to independent BA analyses to check for congruence between these markers.

Morphology

Samples were studied with a Zeiss Axioscope compound microscope operating with differential interference contrast (DIC). Images were obtained with a FLIR camera using open-source software Microscopia Oberta (A. Coloma). Measurements were taken with FIJI win64 ImajeJ software, and reported as follows: maximum value in parentheses, range between the mean plus and minus the standard deviation, minimum value in parentheses, and the number of elements measured in parentheses. For some images of conidiophores, the image stacking software Zerene Stacker v. 1.04 (Zerene Systems LLC, Richland, WA, USA) was employed. Morphological descriptions were based on fertile cultures growing on 2 % MEA at room temperature. Scanning electron microscopy (SEM) images were taken with a Hitachi SU 5000 device with controlled pressure (Hitachi High-Technologies Europe, Germany) at the Centre de Microscopie INRAE/ Université de Bourgogne.

RESULTS

Phylogeny

The analysis of *Apiosporaceae* and related families in the order *Amphisphaeriales* based on 5.8S-ITS2, LSU, *tef1* and *tub2* exons (Fig. 1) revealed that samples of *Arthrinium* group in two significantly different clades, with the genus *Nigrospora* (type species *Nigrospora panici*) being the closest known relative. The three genetic clades form a monophyletic group, which is identified with the family *Apiosporaceae*. The existence of two different genetic clades containing species of *Arthrinium* was already noticed previously (Pintos *et al.* 2019). One clade (*Arthrinium s. str.*) contains the type species of *Arthrinium*, *Ar. caricicola* (epitype CBS H-24083, Crous *et al.* 2020), as well as other samples found growing on *Cyperaceae*, *Juncaceae* and *Poaceae* hosts in temperate, cold or alpine habitats, identified here as *Ar. austriacum*, *Ar. luzulae*, *Ar. morthieri*,

Ar. puccinioides, *Ar. sphaerospermum*, *Ar. cf. sporophleoides* and *Ar. sporophleum*, as well as a new species described below. The other clade contains all sequenced samples of the sexual morph (identified as *Ap. tintinnabula*, *Ap. sinense*, *Ap. montagnei*, *Ap. setosa*, or *Ap. bambusae* = *Ar. hysterinum*), as well multiple samples of arthriniium-like species growing on *Poaceae* and other plant host families worldwide (including tropical and subtropical regions).

The separate analysis of ITS, LSU, and exon data from *tef1* and *tub2* genes from *Apiosporaceae* did not reveal any significant incongruence between these markers (data not shown). LSU alone is enough to discriminate the three genera of *Apiosporaceae*, while 5.8S-ITS2 provides significant support for *Nigrospora* and *Arthrinium s. str.* The *tub2* exon sequences alone support a monophyletic origin of *Nigrospora* and *Apiospora* (but not *Arthrinium*), while the addition of data from intron 5 provides significant support for the three genera. Similarly, the short sequences analysed of *tef1* exon between introns 1 and 2 (about 140 bp) support only *Arthrinium s. str.* (but not *Apiospora* or *Nigrospora*), while the analysis of the 5' extreme of the *tef1* exon between introns 2 and 3 (about 400 bp, available only from 22 samples of *Arthrinium* and *Apiospora* but not from *Nigrospora*), significantly supports an independent origin of these genera. Finally, *tef1* intron 2 is apparently absent in all species of *Apiospora* (but present in both *Arthrinium* and *Nigrospora*), while *tub2* intron 4 is apparently absent in *Nigrospora* (but present in *Apiospora* and *Arthrinium*).

The analysis of *Arthrinium s. str.* based on ITS and LSU, as well as the *tef1* exon between introns 2 and 3 and *tub2* data (introns 3–5 with intermediate exons, plus the 5' extreme of exon between introns 5–6), revealed the existence of two significantly distinct major clades within this genus (Fig. 2). One of them contains the type species, *Ar. caricicola*, as well as two significantly supported groups, one including samples identified as *Ar. japonicum*, *Ar. sporophleum* and *Ar. cf. sporophleoides*, and the other containing samples identified as *Ar. curvatum*, *Ar. luzulae* and *Ar. sphaerospermum*, as well as several undetermined lineages. The other major clade contains samples identified as *Ar. austriacum*, *Ar. morthieri*, *Ar. puccinioides* (which has two significantly different, but apparently cryptic, genetic lineages), and a clade with two undetermined samples. The exact genetic boundaries of several species (*e.g.* *Ar. luzulae*, *Ar. sphaerospermum*, *Ar. sporophleum*) could not be resolved properly, probably due to the lack of complete data from the records in public databases.

On the basis of the genetic results outlined, the taxonomy of *Arthrinium* is revisited below. The genus *Arthrinium* is identified with the clade containing the type species, *Ar. caricicola*, and samples found in temperate, cold or alpine habitats. The clade containing samples of arthriniium-like species occurring worldwide (including tropical and subtropical habitats) is identified as *Apiospora*, and the species nested inside are therefore combined to this genus. The identity of the type species, *Ap. montagnei*, is discussed below, and a lectotype of its basionym, *S. apiospora*, selected among the original collections of this species maintained at PC. Species of *Arthrinium* sequenced for the first time in this study are re-described, and a new name is introduced for one of these lineages.

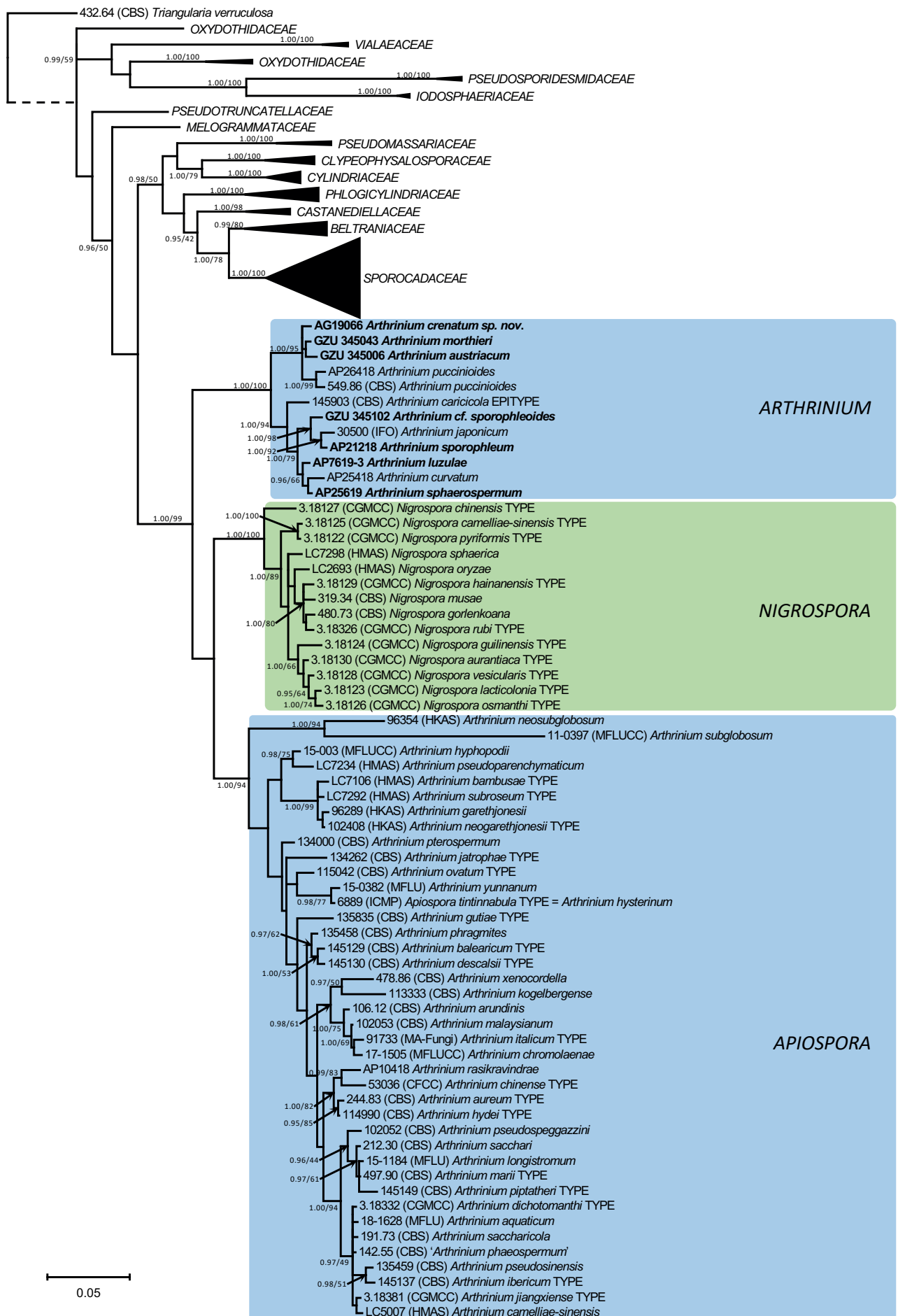


Fig. 1. Majority rule consensus (50 %) ITS rDNA- 28S rDNA- *tub2* exons- *tef1* exons phylogram of the *Amphisphaeriales* obtained in MrBayes from 65 500 sampled trees. Nodes were annotated if supported by > 0.95 Bayesian PP (left) or > 70 % ML BP (right).

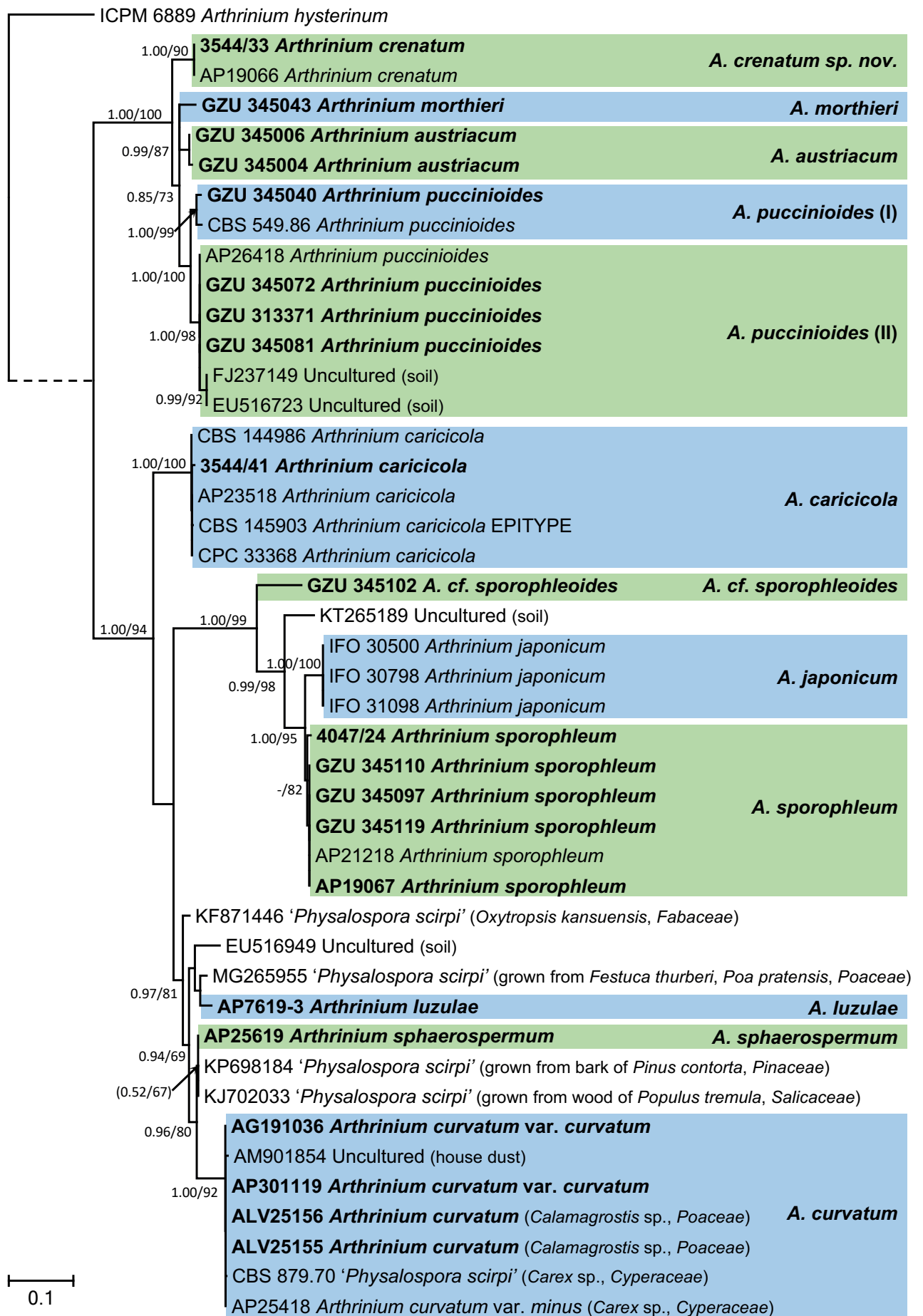


Fig. 2. Best scoring ITS rDNA- 28S rDNA- *tub2*- *tef1* phylogram of the *Apiosporaceae* obtained in RAxML. Nodes were annotated if supported by > 0.95 Bayesian PP (left) or > 70 % ML BP (right). Non-significant support values are exceptionally represented inside parentheses.

Taxonomy

Apiospora Sacc, *Atti Soc. Veneto-Trent. Sci. Nat.* **4**: 85. 1875.

Type species: Apiospora montagnei Sacc., *Atti Soc. Veneto-Trent. Sci. Nat.* **4**: 85. 1875.

Sexual morph: Stromata forming black, linear, confluent, raised areas on host surface, with the longer axis broken at the apex revealing the ostioles of pseudothecia. *Ascomata* uniseriate or irregularly arranged beneath stromata, pseudothecial, black, globose to subglobose with a flattened base. *Peridium* composed of several layers of brown cells arranged in *textura angularis*, with a conspicuous periphysate ostiole. *Hamathecium* paraphyses hyaline, septate, deliquescing early. *Asci* unitunicate, broadly cylindrical, clavate or subglobose, pedicel indistinct, apically rounded. *Ascospores* apiosporic, clavate to fusoid with narrowly rounded ends, composed of a large upper cell and small lower cell, slightly curved, hyaline, smooth-walled, surrounded by a gelatinose sheath, with a large droplet at the centre of the upper cell.

Hyphomycetous asexual morph: Colonies compact, pulvinate, rounded, linear, effused becoming confluent, black. *Mycelium* partly superficial in young colonies, the superficial mycelium is hyaline, with age the cells turn brown, partly immersed in the substrate. *Conidiophore mother cell* formed densely from superficial hyphae, shape swollen, doliiform, subspherical, ovoid, barrel-shaped, flask-shaped, clavate or lageniform, hyaline to brown. *Conidiophores* basauxic, cylindrical, flexuous, unbranched, straight, hyaline, usually aseptate. *Conidiogenous cells* ampulliform to cylindrical, with tiny denticles, hyaline. *Conidia* in face view clavate, oval, elliptical, globose, subglobose, ellipsoid, subcylindrical, lobed, dentate or polygonal; in side view lenticular, with a pale equatorial slit; pale brown to brown, smooth to finely roughened, granular, or minutely guttulate. *Sterile cells* elongated, rolled up, lobed, flattened, hemispherical, usually bigger than conidia, brown. *Setae* present or absent erect, smooth, subcylindrical, tapering to the apex, septate, brown, intermingled among conidiophores.

Coelomycetous asexual morph: Conidiomata acervular, dark brown, partly immersed, becoming erumpent to superficial, parallel to the long axis of the host, opening by longitudinal splitting of the epidermis and revealing a black conidial mass. *Conidiomata wall* composed of several layers of dark brown to brown to hyaline cells arranged as *textura angularis*. *Conidiophore mother cells* arising in dense packs from a mat of brown hyphae emerging directly from the host, shape ranging from ampulliform to doliiform, lageniform, dome-shaped or cylindrical, hyaline to light brown, smooth, producing a single conidiophore. *Conidiophores* basauxic, strait to flexuous, verrucose or smooth, aseptate or with 1–2 septa. *Conidiogenous cells* hyaline, with tiny denticles. *Conidia* 1-celled, globose to obovoid, lenticular, elongated or ellipsoidal; dark brown, smooth-walled, with a thin longitudinal hyaline germ-slit, with a central scar at the base. *Sterile cells* gray, irregularly angled and lobed.

Notes: The name *Apiospora* Sacc. was considered confusingly similar to *Apiosporium* Kunze (type species *Apiosporium salicis*) by Kuntze (1891), who proposed *Detonina* as replacement

name. The Art. 53.3 of the International Code of Nomenclature for fungi, algae, and plants (Turland *et al.* 2018), does not specify the reasons for which two names should be considered confusing, other than being applied to related taxa (especially congeneric species) or commemorate the same person. The type species of *Apiosporium*, *Apiosporium salicis*, is currently thought to belong to *Capnodiaceae* (*Dothideomycetes*), as possible synonym of *Capnodium salicinum* (Chomnunti *et al.* 2011). A proposal to preserve *Capnodium* over *Apiosporium* and other genera was already made, but rejected because of the lack of information from most types (Rogers 1950). Because of these reasons, *Apiosporium* can hardly be confused with *Apiospora*, and so the replacement name is here considered superfluous.

Morphologically, the sexual morphs of *Apiospora* (and the putative sexual morph of *Arthrimum s. str.*, *Pseudoguignardia scirpi* = *Ar. curvatum*) have a large upper cell and a small basal cell. The sexual genera *Scirrhella* and *Rhabdostroma*, each based on a different variety of *Scirrhella curvispora* Speg., were synonymized with *Apiospora* by Rehm (1914) and von Höhnell (1919), respectively. These genera were characterised by their stromata, composed of compressed pseudothecia, but differed in their spore size. The sexual morph of the closely related genus *Nigrospora*, *Khuskia* (type species, *K. oryzae* = *N. oryzae*), also has stromata containing compressed pseudothecia, unitunicate asci surrounded by abundant septate paraphyses, and fusoid to curved unicellular ascospores that form a septum before germinating. Regarding the asexual morphs, those of *Apiospora* and *Arthrimum s. str.* have a basauxic conidiogenesis (Hughes 1953), but in *Apiospora*, conidia are generally more or less rounded in face view and lenticular in side view, while in *Arthrimum*, conidia are variously shaped (globose, angular, polygonal, curved, fusiform, navicular. However, there are some remarkable exceptions to these general trends among species of *Apiospora*, e.g. *Ar. pterospermum* (lobed or dentate conidia) or *Ar. mytilomorphum* (fusoid conidia), and those of *Arthrimum*, e.g. *Ar. globosum* and *Ar. sphaerospermum* (globose conidia). In addition, the conidiophores of several *Arthrimum* species have thick blackish septa, rarely observed in *Apiospora* (Ellis & Ellis 1951), while asexual morphs of *Apiospora* sometimes develop forming acervuli, a feature not observed yet in any species of *Arthrimum*. Finally, the asexual morph of the closely related genus *Nigrospora* usually has cylindrical or lenticular conidia, but lacks the characteristic basauxic conidiogenesis.

Regarding their ecology, *Apiospora* was first thought to be associated mainly with *Poaceae* (von Arx 1952, Müller & von Arx 1962), but the asexual morphs linked to this genus suggest a much wider host range (Ellis & Ellis 1951, Ellis 1965), including a species associated with *Cyperaceae* in the Southern Hemisphere (*Ar. pterospermum*, growing on *Machaerina* and *Lepidosperma*). Most sequenced collections of *Arthrimum s. str.* have been found associated with *Cyperaceae* and *Juncaceae*, and these hosts seem to be also the most frequent among samples of these species identified by previous authors (Ellis & Ellis 1951, Cooke 1954, Scheuer 1996, Minter & Cannon 2018). However, this seems to also be a loose association, as reports of *Arthrimum s. str.* from other plants (including *Poaceae*) are also known. Species of *Apiospora* have been found worldwide, from tropical and subtropical areas to Mediterranean, temperate and cold regions, while reports of *Arthrimum s. str.* from tropical and subtropical habitats are quite rare, and none of them has been confirmed yet. The closely related genus *Nigrospora* seems to be present in tropical regions associated with multiple host

families, e.g. *Brassicaceae*, *Ericaceae*, *Lauraceae*, *Musaceae*, *Poaceae*, *Rosaceae* or *Theaceae* (Wang *et al.* 2017).

Apiospora montagnei Sacc., *Atti Soc. Veneto-Trent. Sci. Nat.* **4**: 85. 1875. Fig. 3.

Synonyms: *Sphaeria apiospora* Durieu & Mont., *Expl. Sci. Alg., Fl. Algér.* **1**, livr. 13: 492. 1849.

Hypopteris apiospora (Durieu & Mont.) Berk., *Hooker's J. Bot. Kew Gard. Misc.* **6**: 227. 1854.

Sexual morph: *Stromata* solitary to gregarious, immersed to erumpent, fusiform, with the long axis broken at the top by one or two cracks, $0.5\text{--}4 \times 0.2\text{--}0.5$ mm ($n = 20$). *Ascomata* uniseriate or irregularly arranged beneath stromata, pseudothecial, black, globose to subglobose with a flattened base, $150\text{--}200$ μm high \times $200\text{--}300$ μm wide. *Peridium* composed of 5 or 6 layers of brown to hyaline cells arranged in *textura angularis*, with a conspicuous periphysate ostiole. *Hamathecium* paraphyses hyphae-like, up to 4 μm wide. *Asci* broadly cylindrical, clavate, with an indistinct pedicel, rounded at the apex, lacking apical apparatus, $72\text{--}115 \times 14\text{--}18$ μm . *Ascospores* uniseriate or biseriate, clavate to fusiform, straight or slightly curved, with narrowly rounded ends, composed of a large upper cell and a small lower cell, hyaline, smooth-walled, measuring $21\text{--}25 \times 6\text{--}8$ μm .

Specimens examined: **Algeria**, Algiers, undated, M.C. Durieu de Maisonneuve (PC FUSION91533); *ibid.* (PC FUSION91536); *ibid.* (PC

FUSION91538); *ibid.* (PC FUSION91542); unknown locality, undated (Fungarium Montagne, PC FUSION91537); *ibid.* (Fungarium Montagne, PC FUSION91541). **Algeria/France** (mixed collection), Perpignan and Algiers, in culms of *Arundo mauritanica*, J.P.F.C. Montagne (Fungarium Montagne, PC MC5210). **France**, Perpignan, in culm of *Arundo 'mauritanica'*, undated, J.P.F.C. Montagne, MC5216 (**lectotype** of *Sphaeria apiospora* designated here PC 0125160, MBT395682); *ibid.* MC5220 (PC).

Notes: The exact genetic identity of *Ap. montagnei* (a replacement name proposed to avoid creating a tautonym from the replaced synonym *Sphaeria apiospora*, Saccardo 1875) cannot be resolved yet, because there are multiple species with very similar sexual morphs, a problem found in many other species of *Apiospora* (Hudson *et al.* 1976). Hudson (1960, 1963a) identified specimens found in Jamaica growing on *Saccharum officinarum* and *Bambusa vulgaris* as *Ap. montagnei*, and obtained an asexual morph identified as *Papularia arundinis*. This putative synonymy was largely followed after his works, despite that the host species were quite different from those mentioned in the original protologues. Bory de Saint-Vincent & Durieu de Maisonneuve (1849) reported that *Sphaeria apiospora* grows in culms of "*Arundo mauritanica*" near Perpignan (France) and the Bouzareah suburb of Algiers (Algeria), as well as on *Piptatherum multiflorum* plants in the Maison-Carrée suburb (currently known as El Harrach) of Algiers (Algeria). The host plant "*Arundo mauritanica*" should refer to *Arundo mauritanica*

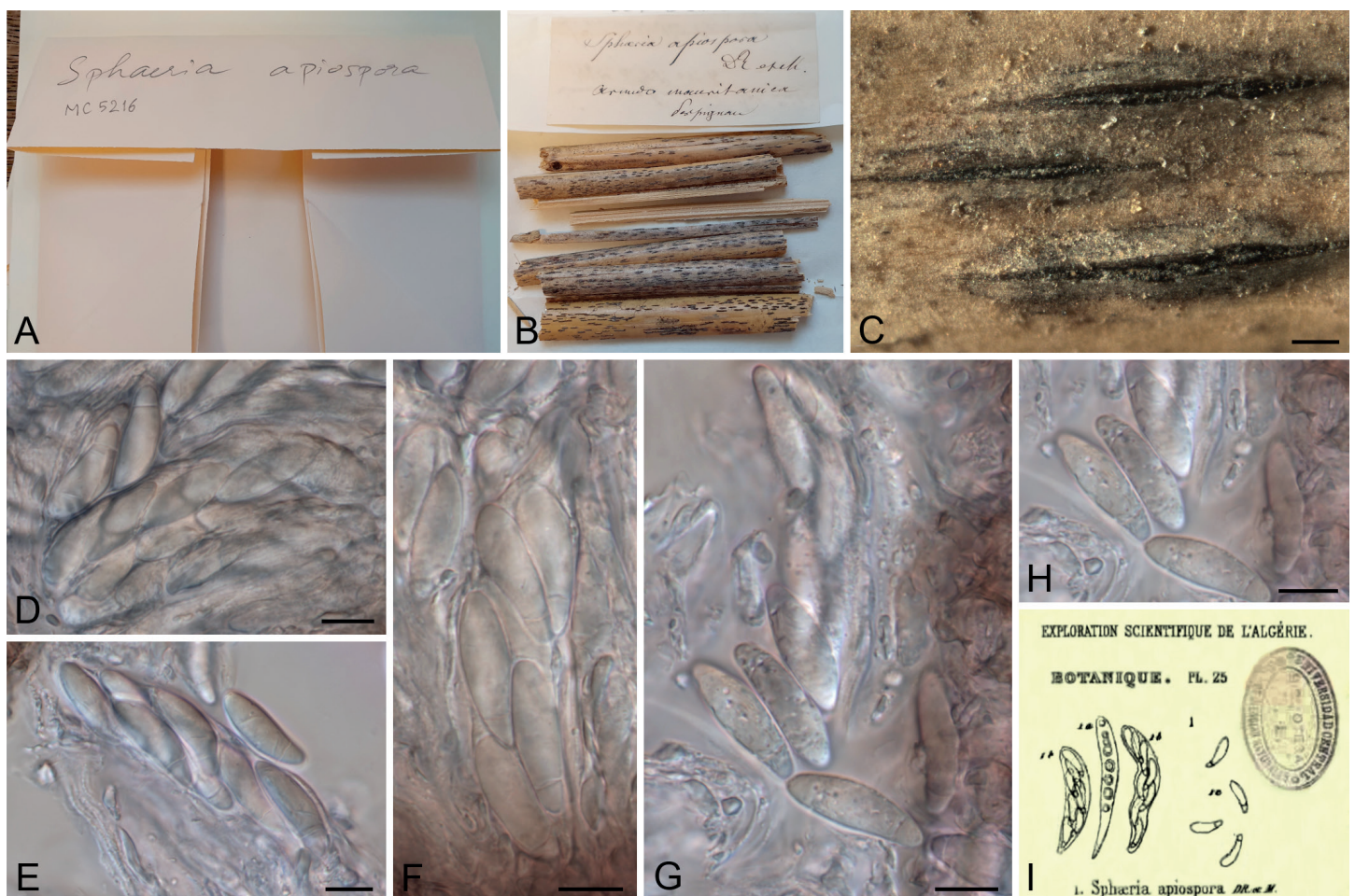


Fig. 3. *Apiospora montagnei* (Montagne MC 5216, PC 0125160 lectotype of *S. apiospora*). **A.** Envelope at PC. **B.** Plant host (*Arundo* sp.) with stromata. **C.** Detail of stromata on host surface. **D–F.** Asci with ascospores. **G–H.** Ascospores. **I.** Asci and ascospores depicted in the protologue. Scale bars: C = 200 μm , D–H = 10 μm .

(Poiret 1789), later combined as *Ampelodesmos mauritanicus* (Durand & Schinz 1895), but most probably it refers to the illegitimate homonym *Arundo mauritanica* (Desfontaines 1798–1799), likely *Arundo aff. plinii* (Danin 2004). Poiret's legitimate binomial *Arundo mauritanica* was at that time subsumed under *Amp. tenax* (Link 1827), a plant cited by Bory de Saint-Vincent & Durieu de Maisonneuve (1849) as host of other fungi, and Link's approach is explicitly followed in a later work by Cosson & Durieu de Maisonneuve (1854). The host plants of the original collections from Perpignan stored at the Fungarium of Paris (PC) were checked, confirming that these were species of the genus *Arundo*, not *Ampelodesmos*. Hardion *et al.* (2012a, 2014) conducted extensive genetic studies on *Arundo aff. plinii* populations and fungarium specimens, and concluded that three distinct lineages could be discriminated: *Arundo plinii s. str.* restricted to Italy, Croatia, Albania and Greece, *A. micrantha* with a circum-Mediterranean distribution, and *A. donaciformis* restricted to southern France and Italian Liguria. Specimens of *A. micrantha* and *A. donaciformis* have been collected near Narbonne, not far from one of the original collection sites of *Sphaeria apiospora* at Perpignan. Therefore, both species could have been the original host of this fungus.

Crous & Groenewald (2013) and Pintos *et al.* (2019) provided a first insight of the genetic diversity of *Apiospora* (as *Arthrinium*) in the Mediterranean region, studying samples obtained from the original host genera reported for *Ap. montagnei*, *Arundo* and *Piptatherum*. At least three species, *Ar. marii*, *Ar. phragmitis*, and *Ar. piptatheri* were found in *Piptatherum miliaceum*, while another four, *Ar. ibericum*, *Ar. italicum*, *Ar. marii* and *Ar. phragmitis* were found in *Arundo* spp. Three out of these five species, *Ar. ibericum*, *Ar. italicum* and *Ar. piptatheri*, seem to be relatively rare, while the other two, *Ar. marii* and *Ar. phragmitis* are more or less widespread. Asci and ascospore size of the sexual morph of both species (Pintos *et al.* 2019) are comparable with those observed in the lectotype collection of *S. apiospora* (\equiv *Ap. montagnei*) from Perpignan chosen here (PC 0125160, MBT395682): asci 70–110 μ m, ascospores 21–25 μ m. These measurements are comparable also with those observed by Hyde *et al.* (1998) in another sample collected by Durieu de Maisonneuve in Algeria (stored also at PC), which has ascospores 23–28 μ m. Therefore, *Ar. marii* and *Ar. phragmitis* are, by now, the most probable matches of *Ap. montagnei*. However, additional samples from *Arundo* and *Piptatherum* plants growing near the type locality (Perpignan) are needed to confirm if other species occur in these hosts. The sequences identified as *Ap. montagnei* in public databases, e.g. ICMP 6967 (isolated from *Bambusa* sp. growing in New Zealand) or CBS 212.30 (from *Phragmites australis* growing in UK), do not seem to match any of the species found by Pintos *et al.* (2019) in *Arundo* or *Piptatherum*, but this could be due to the incomplete data available from these collections. Putative heterotypic synonyms can be found in Müller & von Arx (1962) and Kirk (1991).

Apiospora aquatica (Z.L. Luo *et al.*) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837741.

Basionym: *Arthrinium aquaticum* Z.L. Luo *et al.*, *Fungal Diversity* **1**: 179. 2019.

Apiospora arundinis (Corda) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837742.

Basionym: *Gymnosporium arundinis* Corda, *Icon. fung.* **2**: 1. 1838.

Synonyms: *Papularia arundinis* (Corda) Fr., *Summa veg. Scand.* 509. 1849.

Coniosporium arundinis (Corda) Sacc., *Syll. fung.* **3**: 759. 1884.

Melanconium sphaerospermum subsp. *arundinis* (Corda) Grove, *Bull. Misc. Inf. Kew*: 173. 1918.

Arthrinium arundinis (Corda) Dyko & B. Sutton, *Mycotaxon* **8**: 119. 1979.

Apiospora aurea (Calvo & Guarro) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837675.

Basionym: *Arthrinium aureum* Calvo & Guarro, *Trans. Brit. Mycol. Soc.* **75**: 156. 1980.

Apiospora balearica (Pintos & P. Alvarado) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837665.

Basionym: *Arthrinium balearicum* Pintos & P. Alvarado, *MycKeys* **49**: 24. 2019.

Apiospora camelliae-sinsensis (M. Wang *et al.*) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837666.

Basionym: *Arthrinium camelliae-sinensis* M. Wang *et al.*, *MycKeys* **34**: 11. 2018.

Apiospora chromolaenae (Mapook & K.D. Hyde) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837667.

Basionym: *Arthrinium chromolaenae* Mapook & K.D. Hyde, *Fungal Diversity* **101**: 138. 2020.

Apiospora descalsii (Pintos & P. Alvarado) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837668.

Basionym: *Arthrinium descalsii* Pintos & P. Alvarado, *MycKeys* **49**: 28. 2019.

Apiospora dichotomanthi (M. Wang & L. Cai) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837669.

Basionym: *Arthrinium dichotomanthi* M. Wang & L. Cai, *MycKeys* **34**: 12. 2018.

Apiospora esporlensis (Pintos & P. Alvarado) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837670.

Basionym: *Arthrinium esporlense* Pintos & P. Alvarado, *MycKeys* **49**: 30. 2019.

Apiospora gaoyouensis (C.M. Tian & N. Jiang) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837671.

Basionym: *Arthrinium gaoyouense* C.M. Tian & N. Jiang, *Fungal Syst. Evol.* **2**: 3. 2018.

Apiospora garethjonesii (D.Q. Dai & H.B. Jiang) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837672.

Basionym: *Arthrinium garethjonesii* D.Q. Dai & H.B. Jiang, *Mycosphere* **7**: 1337. 2017.

Apiospora guizhouensis (M. Wang & L. Cai) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837673.

Basionym: *Arthrinium guizhouense* M. Wang & L. Cai, *MycKeys* **34**: 13. 2018.

Apiospora hispanica (Larrondo & Calvo) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837674.

Basionym: *Arthrinium hispanicum* Larrondo & Calvo, *Mycologia* **84**: 476. 1992.

Apiospora hydei (Crous) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837676.

Basionym: *Arthrimum hydei* Crous, *IMA Fungus* **4**: 142. 2013.

Apiospora hyphopodii (D.Q. Dai & K.D. Hyde) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837677.

Basionym: *Arthrimum hyphopodii* D.Q. Dai & K.D. Hyde, *Fungal Diversity* **73**: 112. 2015.

Apiospora hysterina (Sacc.) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837743.

Basionym: *Melanconium hysterinum* Sacc., *Bol. Soc. Broteriana* **11**: 27. 1893.

Synonyms: *Scyphospora hysterina* (Sacc.) Sivan., *Trans. Brit. Mycol. Soc.* **81**: 331. 1983.

Arthrimum hysterinum (Sacc.) P.M. Kirk, *Trans. Brit. Mycol. Soc.* **86**: 409. 1986.

Apiospora iberica (Pintos & P. Alvarado) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837678.

Basionym: *Arthrimum ibericum* Pintos & P. Alvarado, *MycKeys* **49**: 34. 2019.

Apiospora intestini (Kajale *et al.*) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837744.

Basionym: *Arthrimum intestini* Kajale *et al.* (as '*gutiae*'), *Persoonia* **35**: 315. 2105.

Apiospora italica (Pintos & P. Alvarado) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837679.

Basionym: *Arthrimum italicum* Pintos & P. Alvarado, *MycKeys* **49**: 36. 2019.

Apiospora jatrophae (R. Sharma *et al.*) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837680.

Basionym: *Arthrimum jatrophae* R. Sharma *et al.*, *Fungal Diversity* **55**: 119. 2012.

Apiospora jiangxiensis (M. Wang & L. Cai) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837681.

Basionym: *Arthrimum jiangxiense* M. Wang & L. Cai, *MycKeys* **34**: 14. 2018.

Apiospora kogelbergensis (Crous) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837682.

Basionym: *Arthrimum kogelbergense* Crous, *IMA Fungus* **4**: 143. 2013.

Apiospora locuta-pollinis (F. Liu & L. Cai) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837763

Basionym: *Arthrimum locutum-pollinis* F. Liu & L. Cai (as '*locuta-pollinis*'), *Mycosphere* **9**: 1094. 2018.

Apiospora longistroma (D.Q. Dai & K.D. Hyde) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837683.

Basionym: *Arthrimum longistromum* D.Q. Dai & K.D. Hyde, *Fungal Diversity* **82**: 62. 2016.

Apiospora malaysiana (Crous) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837684.

Basionym: *Arthrimum malaysianum* Crous, *IMA Fungus* **4**: 144. 2013.

Apiospora marii (Larrondo & Calvo) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837685.

Basionym: *Arthrimum marii* Larrondo & Calvo, *Mycologia* **82**: 397. 1990.

Apiospora mediterranea (Larrondo & Calvo) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837686.

Basionym: *Arthrimum mediterranei* Larrondo & Calvo, *Mycologia* **84**: 476. 1992

Apiospora mytilomorpha (Bhat & W.B. Kendrick) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837762.

Basionym: *Arthrimum mytilomorphum* Bhat & W.B. Kendrick, *Mycotaxon* **49**: 24. 1993.

Apiospora neobambusae Pintos & P. Alvarado, **nom. nov.** MycoBank MB837756.

Synonym: *Arthrimum bambusae* M. Wang & L. Cai, *MycKeys* **34**: 10. 2018.

[to avoid homonymy with *Apiospora bambusae* (Turconi) Sivan., *Trans. Brit. Mycol. Soc.* **81**: 331. 1983.]

Apiospora neochinense Pintos & P. Alvarado, **nom. nov.** MycoBank MB837757.

Synonym: *Arthrimum chinense* C.M. Tian & N. Jiang, *Sydowia* **72**: 78. 2020.

[to avoid homophony with *Apiospora sinensis* K.D. Hyde *et al.*, *Sydowia* **50**: 27. 1998.]

Apiospora neogarethjonesii (D.Q. Dai & K.D. Hyde) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837695.

Basionym: *Arthrimum neogarethjonesii* D.Q. Dai & K.D. Hyde, *Mycosphere* **11**: 424. 2020.

Apiospora neosubglobosa (D.Q. Dai & H.B. Jiang) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837696.

Basionym: *Arthrimum neosubglobosum* D.Q. Dai & H.B. Jiang, *Mycosphere* **7**: 1337. 2017.

Apiospora obovata (M. Wang & L. Cai) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837704.

Basionym: *Arthrimum obovatum* M. Wang & L. Cai, *MycKeys* **34**: 16. 2018.

Apiospora ovata (Crous) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837703.

Basionym: *Arthrimum ovatum* Crous, *IMA Fungus* **4**: 146. 2013.

Apiospora paraphaeosperma (Senan. & K.D. Hyde) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837705.

Basionym: *Arthrimum paraphaeospermum* Senan. & K.D. Hyde, *Fungal Diversity* **80**: 198. 2016.

Apiospora phragmitis (Crous) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837728.

Basionym: *Arthrimum phragmitis* Crous, *IMA Fungus* **4**: 147. 2013.

Apiospora phyllostachydis (C.L. Yang *et al.*) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837729.

Basionym: *Arthrimum phyllostachydis* C.L. Yang *et al.*, *Phytotaxa* **406**: 102. 2019.

Apiospora piptatheri (Pintos & P. Alvarado) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837708.

Basionym: *Arthrimum piptatherum* Pintos & P. Alvarado, *MycKeys* **49**: 40. 2019.

Apiospora pseudoparenchymatica (M. Wang & L. Cai) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837707.

Basionym: *Arthrimum pseudoparenchymaticum* M. Wang & L. Cai, *MycKeys* **34**: 17. 2018.

Apiospora pseudosinensis (Crous) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837709.

Basionym: *Arthrimum pseudosinense* Crous, *IMA Fungus* **4**: 148. 2013.

Apiospora pseudospegazzinii (Crous) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837710.

Basionym: *Arthrimum pseudospegazzinii* Crous, *IMA Fungus* **4**: 149. 2013.

Apiospora pterosperma (Cooke & Masee) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837711.

Basionym: *Coniosporium pterospermum* Cooke & Masee, *Grevillea* **19**: 90. 1891.

Synonyms: *Pteronidium pterospermum* (Cooke & Masee) Grove, *Hedwigia* **55**: 146. 1914.

Arthrimum pterospermum (Cooke & Masee) Arx, *Gen. Fungi Spor. Pure Cult.*: 331. 1981.

Apiospora qinlingensis (C.M. Tian & N. Jiang) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837712.

Basionym: *Arthrimum qinlingense* C.M. Tian & N. Jiang, *Fungal Syst. Evol.* **2**: 5. 2018.

Apiospora rasikravindrae (Shiv M. Singh *et al.*) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837716.

Basionym: *Arthrimum rasikravindrae* Shiv M. Singh *et al.*, *Mycotaxon* **122**: 452. 2013.

Apiospora sacchari (Speg.) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837731.

Basionym: *Coniosporium sacchari* Speg., *Revta. Fac. Agron. Vet. Univ. Nac. La Plata* **2**: 248. 1896.

Synonym: *Arthrimum sacchari* (Speg.) M.B. Ellis, *Mycol. Pap.* **103**: 11. 1965.

Apiospora saccharicola (F. Stevens) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837732.

Basionym: *Arthrimum saccharicola* F. Stevens, *J. Dept. Agric. Porto Rico* **1**: 223. 1917.

Apiospora serenensis (Larrondo & Calvo) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837733.

Basionym: *Arthrimum serenense* Larrondo & Calvo, *Mycologia* **82**: 396. 1990.

Apiospora setostroma (H.B. Jiang *et al.*) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837713.

Basionym: *Arthrimum setostromum* H.B. Jiang *et al.*, *Asian J. Mycol.* **2**: 260. 2019.

Apiospora sphaerosperma (Pers.) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837962.

Basionym: *Stilbospora sphaerosperma* Pers., in *Usteri Ann. Bot.* **15**: 31. 1795.

Synonyms: *Melanconium sphaerospermum* (Pers.) Link, in *Willdenow Linn. Sp. Pl.*, **6**(2): 91. 1825.

Papularia sphaerosperma (Pers.) Höhn., *Sitzungsber. Kaiserl. Akad. Wiss. Wien. Math.-naturw. Kl., Abt. 1* **125**: 114. 1916.

Notes: Ellis (1965) considered *Gymnosporium phaeospermum* (found in pine wood) a synonym of the earlier species *Stilbospora sphaerospora* (found on tree bark) and *Stilbospora sphaerosperma* (found on *Arundo* and *Phragmites*). He probably used Corda's name as basionym to combine this species into *Arthrimum* because of the putative homonymy of Persoon's epithets with *Ar. sphaerospermum* Fuckel. Since *Ar. sphaerospermum* is a species of *Arthrimum s. str.*, Persoon's epithets are available again for *Apiospora*. However, the woody substrates where *G. phaeospermum* and *S. sphaerospora* were found do not fit well with the hosts of other species of *Apiospora*. Until further evidence is found, only *Stilbospora sphaerosperma* is combined into this genus. Saccardo (1884) reported that this species (as *Melanconium sphaerospermum*) has conidia 8–10 µm diam in face view, and 6–7 µm diam in side view. These measurements fit with the clade identified as *Ar. phaeospermum sensu* Ellis by Crous & Groenewald (2013), but the one identified as *Ar. phragmitis* could be another possible candidate. Type studies, and additional data from both lineages are needed to provide more informed conclusions.

Apiospora subglobosa (D.Q. Dai & K.D. Hyde) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837715.

Basionym: *Arthrimum subglobosum* D.Q. Dai & K.D. Hyde, *Fungal Diversity* **73**: 112. 2015.

Apiospora subrosea (M. Wang & L. Cai) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837734.

Basionym: *Arthrimum subroseum* M. Wang & L. Cai, *MycKeys* **34**: 18. 2018.

Apiospora thailandica (D.Q. Dai & K.D. Hyde) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837735.

Basionym: *Arthrimum thailandicum* D.Q. Dai & K.D. Hyde, *Fungal Diversity* **82**: 66. 2016.

Apiospora vietnamensis (Hol.-Jech.) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837737.

Basionym: *Nigrospora vietnamensis* Hol.-Jech., *Česká Mykol.* **17**: 19. 1963.

Synonym: *Arthrimum vietnamense* (Hol.-Jech.) Mei Wang & L. Cai, *Persoonia* **39**: 139. 2017.

Apiospora xenocordella (Crous) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837738.

Basionym: *Arthrimum xenocordella* Crous, *IMA Fungus* **4**: 151. 2013.

Apiospora yunnanana (D.Q. Dai & K.D. Hyde) Pintos & P. Alvarado, **comb. nov.** MycoBank MB837739.

Basionym: *Arthrimum yunnanum* D.Q. Dai & K.D. Hyde, *Fungal Diversity* **82**: 69. 2016.

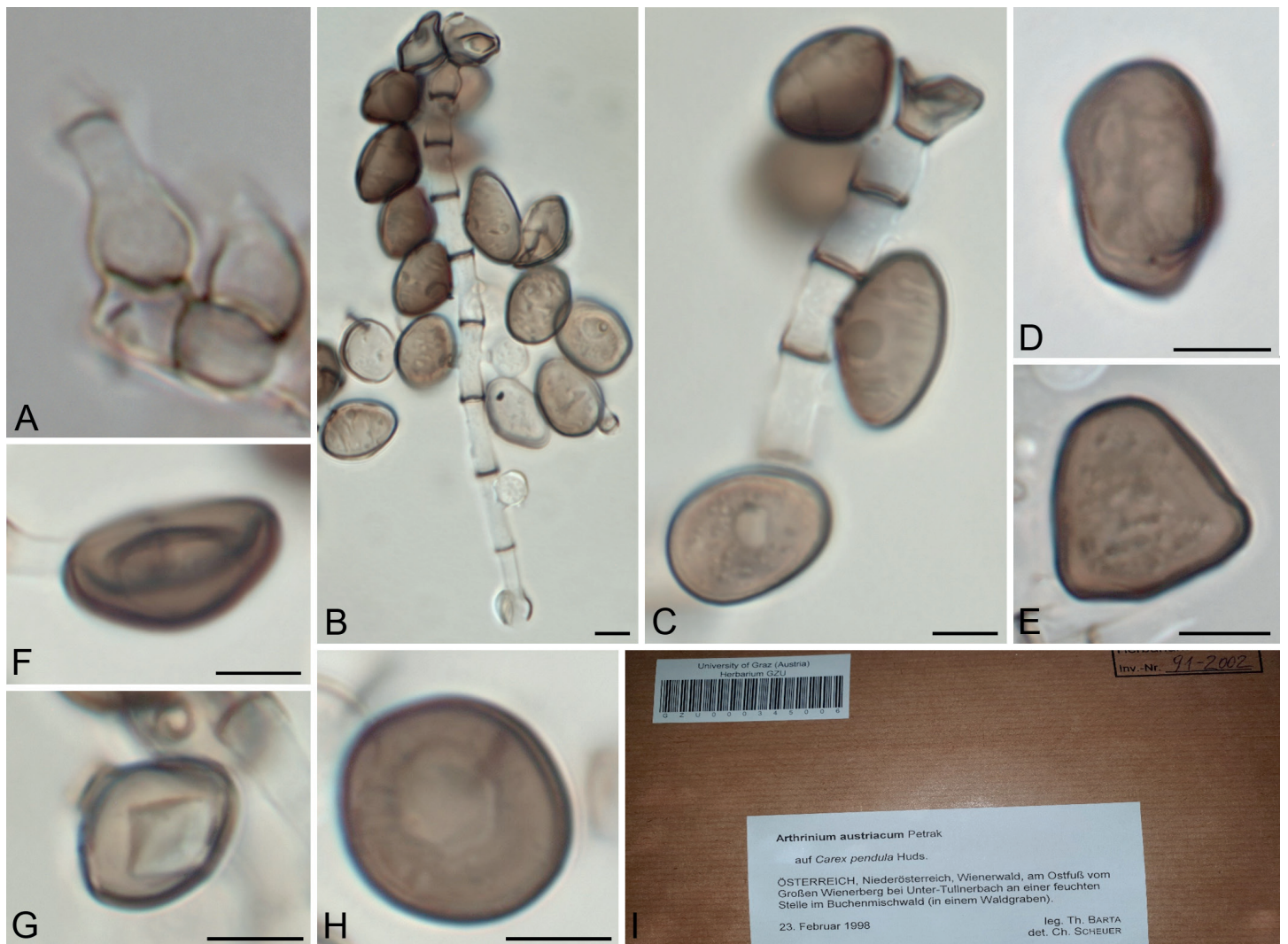


Fig. 4. *Arthrinium austriacum* (GZU 000345006). **A.** Conidiophore mother cells. **B.** Conidiophore mother cell and conidiophore with conidia and sterile cells. **C.** Conidiophore with conidia. **D–F.** Conidia in side view. **G.** Sterile cell with cubical body. **H.** Conidia in face view. **I.** Envelope at GZU. Scale bars = 5 μm .

Arthrinium Kunze & J.C. Schmidt, *Mykol. Hefte* 1: 9. 1817.

Type species: Arthrinium caricicola Kunze & J.C. Schmidt, *Mykol. Hefte* 1: 9. 1817.

Asexual morph. Colonies compact, pulvinate, round, effused becoming confluent, black. *Mycelium* partly superficial (hyaline in young specimens, turning brown with age), and partly immersed in the substratum. *Conidiophore mother cells* originating from superficial hyphae, forming a compact layer, swollen to doliiform, subspherical, ovoid, barrel-shaped, flask-shaped, clavate, or lageniform; hyaline to brown in colour. *Conidiophores* basauxic, cylindrical, flexuous, not branched, straight, hyaline, with brown to dark brown thick transverse septa. *Conidiogenous cells* hyaline, with tiny denticles. *Conidia* unicellular, lateral and sometimes also terminal, in face view variously shaped: polygonal to subglobose, curved, horn-like, flattened, oblong, fusiform, limoniform or lobate; with a distinct hyaline rim and sometimes also concentric rings; in side view hemispherical to triangular or conical; brown to dark brown. *Sterile cells*, terminal or subterminal (same location as conidia), often containing one or more highly refractive cubical bodies, globose to triangular, polygonal, hat-shaped, lobed, lageniform, curved, ellipsoidal or irregularly lobed; paler than conidia. *Setae* absent.

Notes: Sequenced samples of *Arthrinium* s. str. were mostly found on *Cyperaceae* and *Juncaceae*, but also *Poaceae* and other plant hosts. According to the compilation of published records made by Minter & Cannon (2018), *Arthrinium* species occur mainly in temperate, cold or alpine regions of the Northern Hemisphere, including Europe, Turkey, Iran, alpine India, Russia, China, Japan, Canada and the USA, as well as similar areas of the Southern Hemisphere (Argentina, South Africa, New Zealand). Samples found in subtropical and tropical regions could actually be different fungal species, e.g., reports of *Ar. caricicola* from Maharashtra, India (Hande *et al.* 2014) might be *Ap. mytilomorpha*, described from the neighbouring state of Karnataka, since the latter species has fusoid conidia that could resemble the navicular conidia of *Ar. caricicola*. The reports of *Ar. sphaerospermum* in Minter & Cannon (2018) probably represent *Ap. sphaerosperma* (= *Ar. phaeospermum sensu* Crous & Groenewald 2013).

Arthrinium austriacum Petr., *Sydowia* 1: 4. 1959. Fig. 4.

Asexual morph: Colonies punctiform, pulvinate to effuse, sometimes confluent, black, 80–220 (–250) μm diam. *Mycelium* with immersed and superficial layers composed of hyaline to very pale brown, branched and septate hyphae measuring 1.5–5 μm wide. *Conidiophore mother cells* spherical to

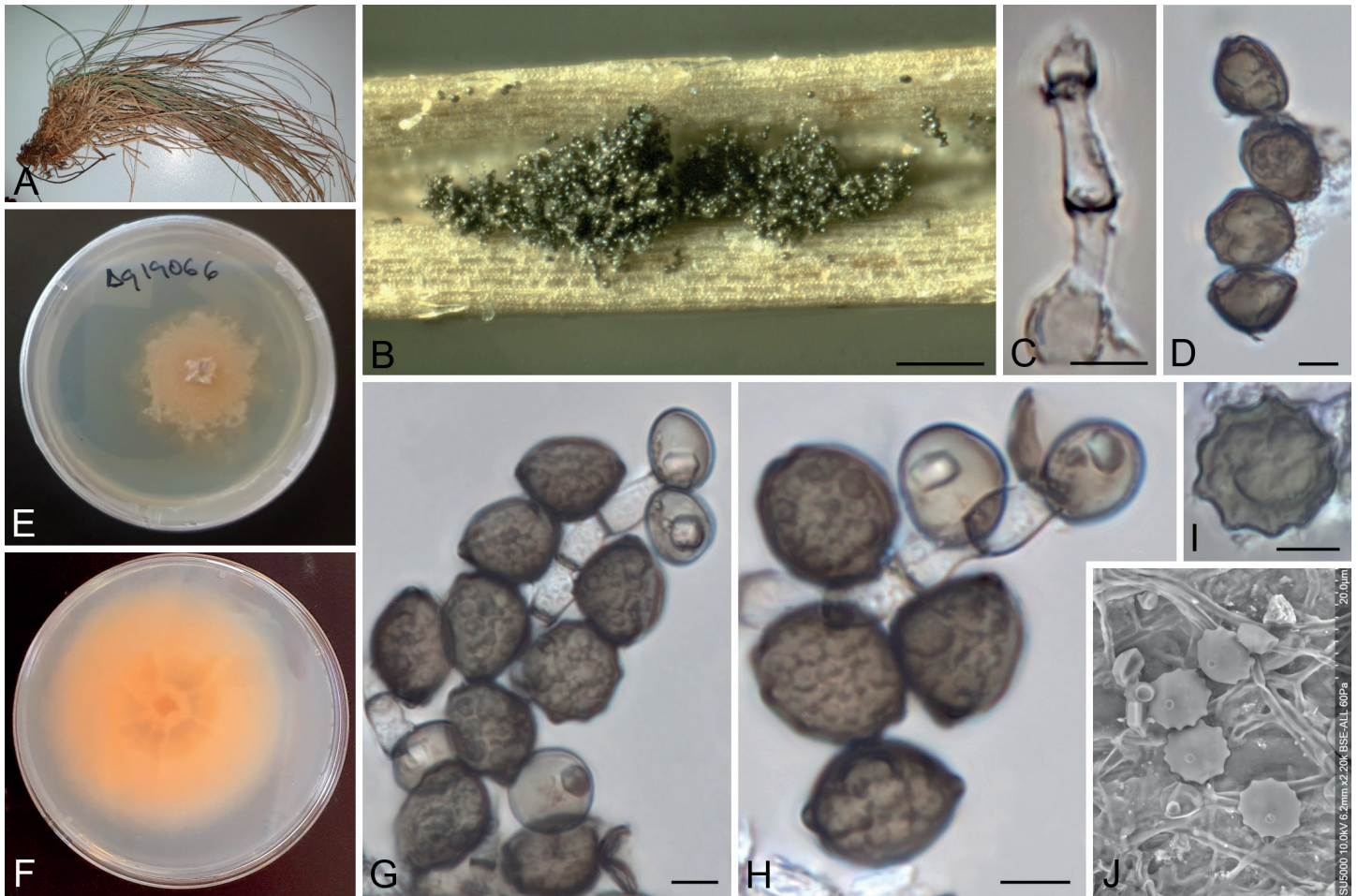


Fig. 5. *Arthrimum crenatum* (AG19066). **A.** Host. **B.** Colony on host surface. **C.** Conidiophore mother cell. **D.** Conidia in side view. **E–F.** Colony growing on MEA. **G–H** Conidia and sterile cells attached to the conidiophore. **I.** Conidia in face view. **J.** Conidia observed with SEM. Scale bars: B = 200 μ m, C–D, G–H = 5 μ m, I = 10 μ m.

ampulliform, 4–6 μ m diam, attached to the superficial mycelium network by an irregularly shaped basal cell 2–4 μ m diam. *Conidiophores* cylindrical, erect or flexuous, 40–100 μ m long, with dark refringent septa. *Conidiogenous cells* hyaline, with inconspicuous denticles between septa. *Conidia* brownish, with two paler concentric rings, in face view irregularly polygonal or rounded and 9–12 μ m diam, in side view irregularly triangular or polygonal and 10–14 \times 8–10 μ m. *Sterile cells* smaller and paler than conidia, globose to ellipsoid, containing large refringent crystalline granules.

Specimens examined: **Austria**, Lower Austria, Wienerwald, eastern foot of the Wienerberg, near Untertullnerbach, on *Carex pendula*, 23 Feb. 1998, *Th. Barta* (GZU 000345006); Styria, Koralmpe, Deutschlandsberger Laßnitz Klause, on *Carex pendula*, 14 Aug. 1996, *M. Heftberger* (GZU 000345004); Upper Austria, Sankt Georgen im Attergau, ca. 13 km SSW of Vöcklabruck, E of Weyregg am Attersee, on *Carex pendula*, 7 Jul. 2002, *H. Teppner* (GZU 000345007).

Notes: The samples analysed in the present study were identified by Scheuer (1996), who compared them with the type material of *Ar. austriacum* [**Austria**, Lower Austria, Georgenberg near Purkersdorf, on *Carex pendula*, Oct. 1943, *F. Von Petrak* (**holotype** W)]. *Arthrimum austriacum* is characterised by the concentric rings of its conidia observed in face view. These rings are present also in *Ar. puccinioides*, but this species has regularly polygonal (never rounded) conidia in face view. In side view, conidia of *Ar.*

austriacum resemble those of *Ar. fuckelii* and *Ar. morthieri* due to their irregularly triangular or polygonal morphology, but *Ar. morthieri* has oblong or irregular conidia in face view.

Arthrimum crenatum Pintos, P. Alvarado & Gardiennet, *sp. nov.* MycoBank MB837755. Fig. 5.

Etymology: From ‘crena’ (Lat. incision, notch), referring to the morphology of conidia in face view, looking like a toothed gear.

Asexual morph with *colonies* compact, scattered, rounded to elongated, 500–1 100 \times 200–500 μ m (length \times width, $n = 10$). *Mycelium* superficial and immersed, composed of hyaline to brown, smooth septate hyphae that branch and anastomose, measuring 2–5 μ m diam. *Conidiophore mother cells* ampulliform to lageniform, measuring 5–9 \times 4–6 μ m (length \times width) ($n = 20$), emerging from a network of hyaline to brown cells. *Conidiophores* cylindrical, straight or flexuous, septate, hyaline excepting for the brown or dark brown thick transverse septa, 25–100 \times 2–4 μ m (length \times width) ($n = 30$), each segment measuring 9–11 μ m long. *Conidiogenous cells* cylindrical, 1–3 \times 1 μ m, occurring between the septa of conidiophores. *Conidia* dark brown, smooth, in face view crenate or stellate, looking like a toothed wheel or a sprocket, 10–12 μ m in diam., in side view polygonal, hemispherical, with wavy-stellate margin and convex apex, 7–9(–10) \times 10–13 (height \times width, $n = 50$). *Sterile cells* spherical to subspherical, with a cubic refringent element 7–10

µm in diam. *Culture characteristics* (day/light 25 °C, after 2 wk): colonies slow-growing, with sparse aerial mycelium, reaching 12 mm in 2 wk. On MEA and PDA, pale salmon on surface, salmon in reverse.

Typus: **France**, Côte-d'Or, Brochon, Champ Sement, on dead leaves of grass (probably *Festuca burgundiana*), 28 Apr. 2019, A. Gardiennet (**holotype** AG19066); ex-type culture CBS 146353.

Additional specimens examined: **France**, Côte-d'Or, Brochon, Champ Sement, on dead leaves of *Carex cf. humilis / halleriana*, 9 Dec. 2014, A. Gardiennet (A. Gardiennet fungarium AG14223). **Germany**, Potsdam, Bornim, SE end of Hugstraße, on leaves of *Carex ciliata*, 29 Sep. 2011, V. Kummer (V. Kummer fungarium VK-P-2529/19b).

Notes: Morphologically, the crenate conidia of *Ar. crenatum* resemble those of *Ap. pterosperma*, but the latter are 12–25 µm diam in face view and have more pointed lobes, while conidia of *Ar. crenatum* are only 10–12 µm diam, and have more rounded lobes. In addition, *Ap. pterosperma* lacks sterile cells. *Apiospora pterosperma* is known to occur on the *Cyperaceae* genera *Machaerina* and *Lepidosperma*, therefore representing an exception to the overall ecological preferences of *Apiospora*.

Arthrinium curvatum Kunze, *Mykol. Hefte* 2: 103. 1823. Fig. 6. *Synonym*: *Camptoum curvatum* (Kunze) Link, in Willdenow *Linn. Sp. Pl.* 6(1): 44. 1824.

Colonies compact, round, often confluent, dark grey to black, 80–520 diam. *Mycelium* superficial and immersed, composed of hyaline to pale brown smooth hyphae 3–7 µm in diam. *Conidiophore mother cells* emerging from superficial hyphae, spherical to lageniform, hyaline with brown pigments at the base, measuring (3–)5–7(–8) × (3–)5–6(–8) µm (n = 30). *Conidiophores* cylindrical, not branched, straight or flexuous, hyaline, smooth, with a single brown transversal septum, measuring 30–100 × 2–4 µm (n = 30). *Conidiogenous cells* cylindrical, measuring 1–1.5 × 1–1.5 µm (n = 20). *Conidia* produced along the sides of conidiophores from well-developed denticles, strongly curved and rounded at the ends, brown coloured with a hyaline germ slit and a conspicuous scar, measuring (9–)11–14(–15) µm long in face view, (5–)6–8(–9) µm in side view (n = 30). *Sterile cells* oblate or rounded, paler than conidia, not containing refringent bodies, 7–8 µm diam.

Culture characteristics: Flat colonies on MEA with moderate aerial mycelium, reverse whitish.

Typus: **Germany**, Saxony, Leipzig, on dead leaves of *Scirpus sylvaticus* (**holotype** HAL 3337F).

Additional specimens examined: **France**, Auvergne, Puy-de-Dôme, Saint-Alyre-d'Arlanc, Le mouline de Chelles, on dead leaves of *Scirpus sylvaticus*, 855 m asl, 22 Apr. 2019, A. Gardiennet (Alain Gardiennet fungarium AG191036), culture CBS 146354; Calvados, Louvières, on dead leaves of *Carex pendula*, 18 Jan. 2020, A. Gardiennet, (Alain Gardiennet fungarium P301119A). **Norway**, Oslo, Wyllerløypa, grassy roadside, on leaves of *Calamagrostis* sp., 15 Apr. 2020, E.W. Johanssen (Edwin W. Johanssen fungarium EWJ24118299); *ibid.*, in a moist slope between a stream and melting water near a ski slope, on leaves of *Calamagrostis* sp., 15 Apr. 2020, E.W. Johanssen, (Edwin W. Johanssen fungarium EWJ24117931). ***Arthrinium curvatum* var. *minus***: **Austria**,

Upper Austria, a bit W of Steyr, Schloss Rosenegg, on dead leaves of *Carex cf. elata*, 300 m asl, 9 Apr. 1982, C. Scheuer (GZU 000345023).

Notes: The samples identified here as *Arthrinium curvatum* var. *curvatum* are identical with the original collection studied (HAL 3337 F), and fit the descriptions made by Ellis & Ellis (1951), Scheuer (1996) and Minter & Cannon (2018). The new specimens were found in both *Cyperaceae* (*Carex*) and *Poaceae* (*Calamagrostis*) hosts, where the putatively related species *Ar. luzulae* and *Ar. sphaerospermum* are thought to occur too (Minter & Cannon 2018). Several undetermined sequences related to those of *Ar. curvatum* have been obtained from very different sources, including *Oxytropis kansuensis* (*Fabaceae*), *Festuca thurberi* and *Poa pratensis* (*Poaceae*), *Pinus contorta* (*Pinaceae*) and *Populus tremula* (*Salicaceae*). Therefore, it seems that the whole clade is associated with a diverse range of host plants. Interestingly, *Ar. curvatum* is supposed to be the only species of *Arthrinium* s. str. from which a sexual morph has been obtained. The sexual morph was obtained by Gutner (1927) on *Scirpus sylvaticus*, and named *Pseudoguignardia scirpi*. Ellis & Ellis (1951) reproduced the experiment with a new variety, *Ar. curvatum* var. *minus*, but further studies on the life cycle of species of *Arthrinium* are needed to understand which hosts (if any) can actually develop a sexual morph of *Arthrinium* s. str. *Arthrinium curvatum* var. *minus* was proposed for specimens presenting curved spores smaller than those of *Ar. curvatum* var. *curvatum*. Minter & Cannon (2018) upgraded this variety to species rank as *Ar. minus*, due to the significant differences between the spore sizes of both varieties, which do not overlap. However, in the present work, specimens of both varieties (AG191036 and AP25418), did not show significant differences in up to three genetic markers (ITS, LSU, *tub2*), and so they are considered the same species until further evidence of reproductive isolation is found.

Arthrinium luzulae M.B. Ellis, *Mycol. Pap.* 103: 18. 1965. Fig. 7.

Colonies punctiform, sometimes confluent, effuse, blackish brown to black, 100–400 µm diam. *Mycelium* superficial and also immersed in the substratum; superficial part composed of smooth-walled, pale to olivaceous brown septate hyphae 2–7 µm thick, branching and anastomosing; immersed part sparse, composed of pale olivaceous brown hyphae 1–4 µm thick. *Conidiophore mother cells* emerging on the mat formed by superficial hyphae, barrel-shaped to lageniform, measuring 4–8 × 3–6 µm. *Conidiophores* erect or erumpent, simple, cylindrical, straight or flexuose, sometimes branched, hyaline, 30–80 µm long and 3–6 µm diam, with multiple thick, brown to dark brown, transversal septa. *Conidia* curved with the ends bent inwards (horn-like), brown to dark brown, with a hyaline germ slit, smooth-walled, 16–21 × 11–15 µm in face view, 8–11 µm thick (side view), tapering at the ends of the horns to 2–4 µm. *Sterile cells* acrogenous, hemispherical, pale brown, 5–11 × 5–7 µm.

Culture characteristics: Flat colonies spreading on MEA with moderate aerial mycelium, reverse yellow.

Specimen examined: **Spain**, Catalonia, Girona, Coll de la Marrana, on dead leaves of *Luzula sylvatica*, 2 470 m asl, 7 Jun. 2019, Á. Pintos (Ángel Pintos fungarium AP7619-3), culture CBS 146356.

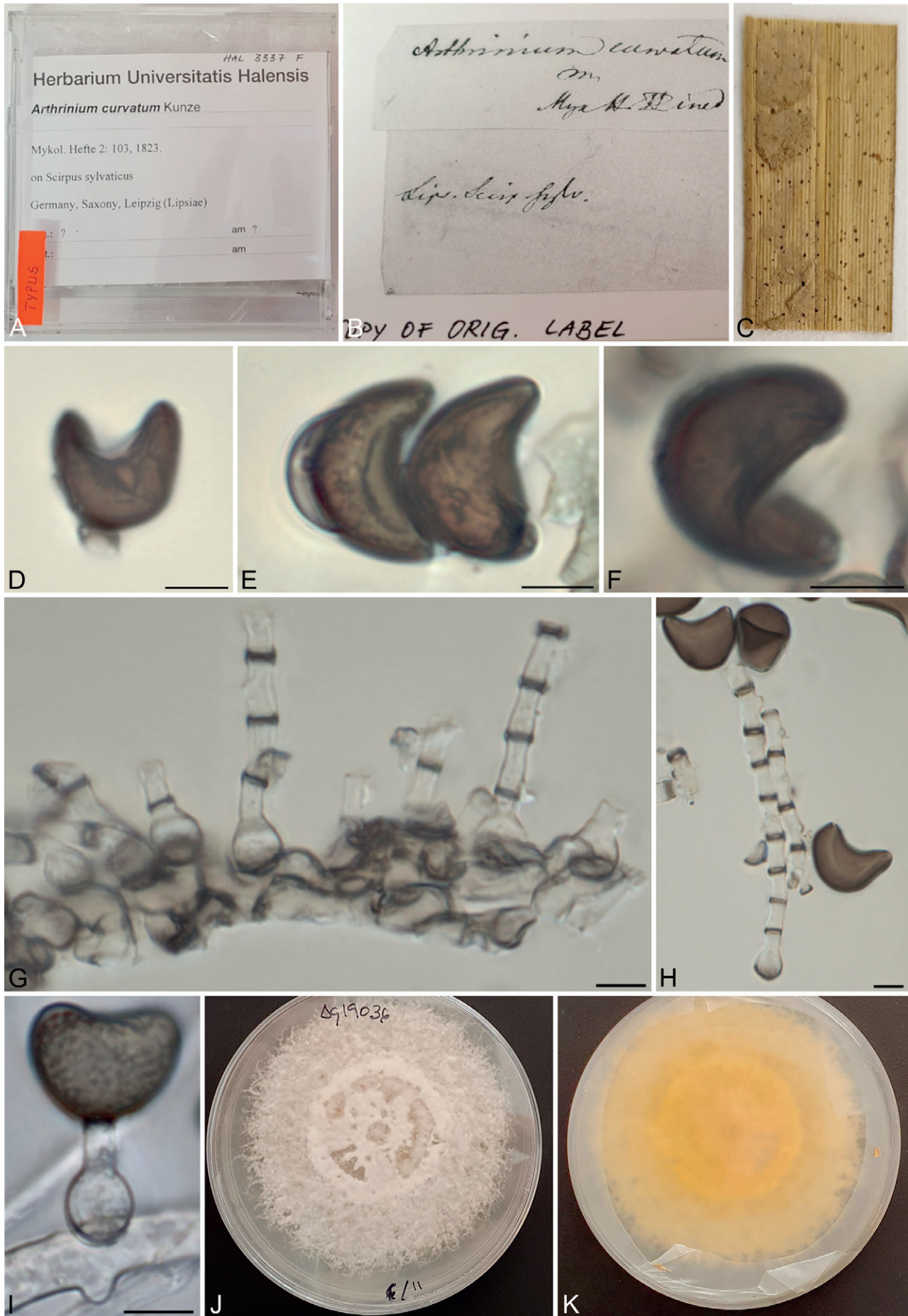


Fig. 6. *Arthrinium curvatum*. **A–F.** (HAL 3337 F). **A.** Envelope at HAL. **B.** Copy of the original label. **C.** Colony on host (*Scirpus sylvaticus*). **D–F.** Conidia. **G–K.** (AG19036). **G.** Conidiophore mother cell. **H.** Conidia attached to conidiophore. **I.** Conidiogenous cell giving rise to conidia. **J–K.** Colony growing on MEA. Scale bars = 5 μ m.

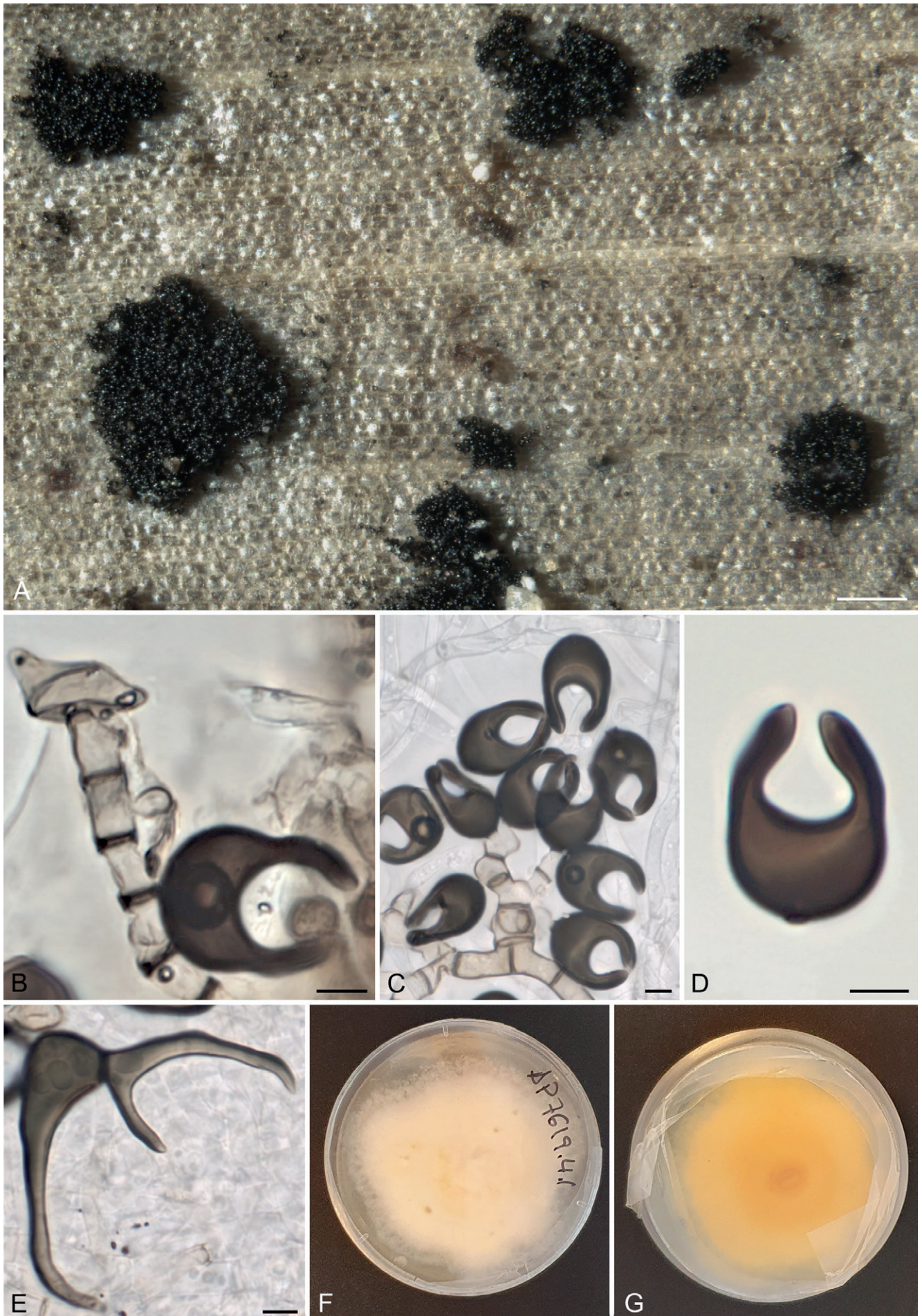


Fig. 7. *Arthrimum luzulae* (AP7619.4.1). **A.** Colony on host surface. **B–C.** Conidia attached to conidiophore. **D.** Conidia in face view. **E.** Aberrant conidia in MEA culture. **F–G.** Colony growing on MEA. Scale bars: A = 200 μm , B–E = 5 μm .

Notes: *Arthrinium luzulae* is the only species with inwardly curved conidia. The non-type specimen identified here matches the descriptions made by Ellis & Ellis (1951), Scheuer (1996) and Minter & Cannon (2018). Genetically, it is related to samples identified as *Ar. curvatum* (which have outwardly-curved conidia), suggesting that the whole clade containing these samples could have an ancestor with curved conidia (a feature not present in the other species of *Arthrinium*). Some samples inside this clade, here identified as *Ar. sphaerospermum* because of their globose conidia, could have reverted to an earlier undifferentiated conidial shape.

Arthrinium morthieri Fuckel, *Fungi Rhen. Exs.*, Suppl. Fasc. 5: no. 1914. 1867. Fig. 8.

Colonies pulvinate, rounded or ovoid, usually 100–300 µm diam, blackish brown in colour. *Mycelium* superficial and also immersed in the substratum, composed of branched and anastomosing, septate hyphae, pale to mid olivaceous brown, smooth-walled, 2–5 µm thick. *Conidiophore mother cells* emerging on the mat formed by superficial hyphae, subspherical or barrel-shaped, lageniform, 5–6 × 4–5 µm *Conidiophores* erect or ascending, simple, straight or flexuous, cylindrical, colourless except for the thick, brown to dark brown, transverse septa, smooth-walled, 30–90 µm long and 2–5 µm wide. *Conidia* flattened, oblong or irregularly rectangular to quadrangular or rhombic in face view, 11–16 × 5–9 µm, in side view triangular or rhombic, 11–16 × 11–16 µm, with a germ slit running along the outer wall. *Sterile cells* spherical to ellipsoidal, very pale, sometimes containing cubical refractive body 6–10 × 5–9 µm.



Fig. 8. *Arthrinium morthieri* (GZU 000345043). **A.** Envelope at GZU. **B,E–F.** Conidia attached to conidiophore. **C,G.** Conidia in face view. **D.** Conidiophore mother cells. **H.** Sterile cell with cubical body. Scale bars = 5 µm.

Specimens examined: **Austria**, Upper Austria, Steyr, a bit N of Schloss Rosenegg, 300 m asl, on *Carex pilosa*, in an alluvial deciduous forest, 9 Jul. 1994, N. Vasilyeva & C. Scheuer (GZU 000345049); Wien, Leopoldsdorf, ESE of Josefinenhütte, on *Carex digitata*, 6 Mar. 1998, Th. Barta (GZU 345043).

Notes: The samples analysed here were identified as *Ar. morthieri* by Scheuer (1996), and they match the descriptions provided by Ellis & Ellis (1951) and Minter & Cannon (2018). Their conidia resemble those of *Ar. fuckelii*, but the latter are about 15–21 × 5–8 µm in side view, vs. 11–16 × 11–16 µm in *Ar. morthieri*. In addition, sterile cells of *Ar. morthieri* lack lateral projections (present in *Ar. fuckelii*).

Arthrinium sphaerospermum Fuckel, *Jb. Nassau. Ver. Naturk.* 27–28: 79. 1874. Fig. 9.

Synonym: *Goniosporium sphaerospermum* (Fuckel) Sacc., *Syll. Fung.* 4: 280. 1886.

Colonies rounded to ovoid, pulvinate, up to 500 µm long, blackish brown. *Mycelium* superficial and also immersed in the substratum; superficial part composed of a network of septate, pale to mid brown, smooth-walled, hyphae, branched and anastomosing, measuring 2–7 µm thick, arranged in two or more layers; immersed hyphae pale to brown, 1–7 µm thick. *Conidiophore mother cells* emerging on the mat formed by superficial hyphae, subspherical to flask-shaped, measuring 5–9 × 4–8 µm. *Conidiophores* erect or erumpent, simple, straight or flexuous, cylindrical, hyaline excepting for the thick, brown to dark brown, transversal septa, smooth-walled, 10–90 µm long and 2–3 µm wide. *Conidia* very densely packed in the conidiophore, globose or subglobose, dark gold to gold-brown in colour, smooth-walled, 6–9 µm diam. *Sterile cells* only seen in culture, cylindrical to oblong or clavate, paler than conidia, measuring 12–30 × 5–8 µm.

Typus: **France**, Jura, on *Phleum pratensis*, Apr. 1872, P. Morthier (**holotype** G 00127277).

Culture characteristics (day/light 25 °C, after 2 wk): Colonies slow-growing, with sparse aerial mycelium, reaching 30 mm in 2 wk. On MEA and PDA, white on surface, salmon in reverse.

Additional specimen examined: **Norway**, Viken, Akerhus, Nittedal, Varingskollen, alpine hill with some snow spots, probably on *Poaceae*, 27 May 2019, S. Moen (Ángel Pintos fungarium AP25619), culture CBS 146355.

Notes: The Norwegian sample identified here as *Ar. sphaerospermum* was compared with the type collection from France (G 00127277). Koskela (1983) reported that conidia of *Ar. globosum* and *Ar. sphaerospermum* look similarly globose in face view and ellipsoid in side view, but those of *Ar. globosum* have a hyaline rim not observed in *Ar. sphaerospermum*. Conidia of *Ar. globosum* are also slightly larger (8–10 µm) than those of *Ar. sphaerospermum* (6–8 µm). In addition, *Ar. globosum* is supposed to be strictly associated to *Cyperaceae*, while *Ar. sphaerospermum* has been found also in *Poaceae*, in the same way as the samples identified here as *Ar. curvatum*. Unfortunately, the original collections of *Ar. globosum* from Koskela could not be located in the OULU fungarium, and so the exact genetic identity of this species remains unresolved.

Arthrinium sporophleoides Fuckel, *Jb. Nassau. Ver. Naturk.* 27–28: 78. 1874. Fig. 10.

Colonies compact, rounded to elongated, scattered or sometimes confluent, up to 600 µm diam. *Mycelium* superficial and also immersed, hyaline to pale brown, composed of smooth hyphae 3–7 µm diam. *Conidiophore mother cells* emerging on the mat formed by superficial hyphae, globose to lageniform, hyaline with brown pigments at the base, measuring 4–8 × 4–9 µm. *Conidiophores* erect or erumpent, simple, straight or flexuous, cylindrical, measuring 30–100 µm long and 2–5 µm wide, hyaline excepting for numerous brown to dark brown thick transversal septa. *Conidia* fusoid in face view, measuring 11–14 × 5–5.5 µm, in side view often triangular or polygonal with a distinct hyaline rim. *Sterile cells* irregularly lobed or subspherical with cubical refringent bodies.

Specimen examined: **Austria**, Styria, Ennstal, Gesäuse, Hartelsgraben, on *Carex firma*, 15 Sep. 1989, P. Zwetko (GZU 000345102, as *Ar. sporophleum*).

Additional specimens examined: **Arthrinium caricicola:** **Germany**, Brandenburg, Potsdam-Mittelmark, Werder (Havel), Phöben, Wachtelberg, on *Carex ericetorum*, 18 Apr. 1999, V. Kummer (Volker Kummer fungarium VK-P-2524/1); Potsdam, Sacrow, 0.5 km NE road to Kladow, on *Carex ericetorum*, 15 Apr. 2004, V. Kummer (Volker Kummer fungarium VK-P-2524/2). **Russia** Leningradskaya Oblast, Lodeinopol' Ski District, 51 km W of Lodéinoe Pole, Nizhnesvirsky nature reserve, Segezha forestry, near the river Svir, on *Carex ericetorum*, wintered leaves, 28 May 1990, V. Mel'nik, (GZU 000345013). **Sweden**, Torne lappmark, Jukkaskärvi, on *Carex vaginata*, 13 Jul. 1986, A. Nograsedk (GZU 000343016). **Arthrinium carinatum:** **Estonia**, Saaremaa Island, near Kihelkonna, on dead leaves of *Carex ericetorum*, 1909, F. Bucholtz, (**holotype** FH Bucholtz 1757). **Arthrinium fuckelii:** **Austria**, Styria, Hochschwab, Aflenzer Staritzen, ca. 16 km S of Mariazell, NW of Seebergsattel, top of Seeleiten, 1700 m asl, on *Carex atrata*, 21 Jun. 1984, J. Hafellner (GZU 000345025). **Romania**, Harghita, Ciuc depression, near Bălan, on *Carex sempervirens*, 1600–1700 m asl, 16 Aug. 1942, A. Boros (GZU 000345026). **Arthrinium muelleri:** **Austria**, Styria, Seetal Alps, Zirbitzkogel, on *Carex foetida*, 1900 m asl, 1959, H. Heske (GZU 000345126); *Ibid.* (GZU 000345136). **Arthrinium naviculare:** **Finland**, Lapponia, NW Enontekiö, N Kovdoskai, alpine meadow, ca. 800 m asl, 1 Jul. 1968, H. Roivainen (CUP 5683). **Arthrinium puccinioides:** **Austria**, Lower Austria, S-slope of Hutberg by Grünbach, on dead twigs of *Carex hordeistichos*, 29 Jun. 1998, Th. Barta (GZU 000345072); Lower Austria, 4.5 km SSW of Hainburg an der Donau, WNW of Bundessportschule Spitzerberg, on *Carex flacca*, 180 m asl, 5 May 2009, Th. Barta (GZU 313371); Styria, Hochschwab, Aflenzer Staritzen, S-slope of Seeleiten, NW of Seebergsattel, on *Carex sempervirens*, 9 Jul. 1997, C. Scheuer (GZU 000345040, as *Ar. morthieri*); Styria, Schladminger Tauern, Kleinsölk-Obertal, Schwarzensee, on *Carex rostrata*, 5 Aug. 1984, C. Scheuer (GZU 000345065); Styria, Schladminger Tauern, Kleinsölk, S of Gröbming, on *Carex rostrata*, 19 Jul. 1986, C. Scheuer (GZU 000345068); Upper Austria, immediately W of Steyr, floodplains of Steyr at Rosenegg, on *Carex flacca*, 19 May 1996, C. Scheuer (GZU 000345081). **Germany**, Brandenburg, Potsdam, Bornim, on dead leaves of *Carex humilis*, Sep. 2011, V. Kummer (GZU 000345086). **Arthrinium sporophleum:** **Austria**, Burgenland, Leithagebirge, on *Carex hordeistichos*, 31 Oct. 2010, Th. Barta (GZU 000345112); Carinthia, immediately W of Krumpendorf am Wörthersee, on *Carex* sp., 2 Nov. 1999, H. Riegler-Hager (GZU 000345119); Styria, Ennstal, Gesäuse Nationalpark, Hartelsgraben, on *Carex firma*, 15 Sep. 1989, P. Zwetko (GZU 000345102); Styria, ca. 8

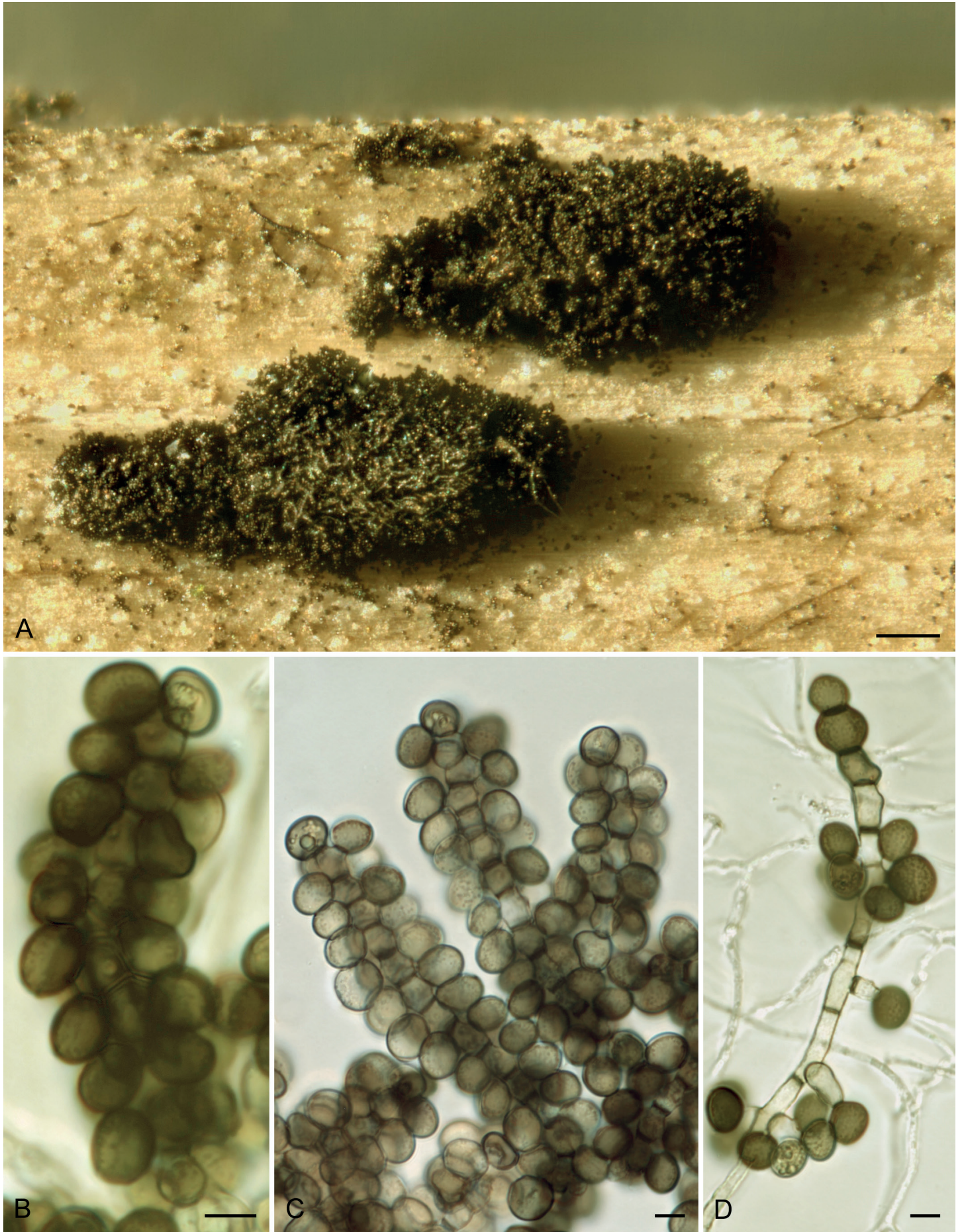


Fig. 9. *Arthrinium sphaerospermum* (AP25619). A. Colony on host surface. B–D. Conidia attached to conidiophore. Scale bars: A = 200 μm, B–D = 5 μm.



Fig. 10. *Arthrimum cf. sporophleoides* (GZU 000345112). **A.** Colony on host surface. **B.** Conidiophore mother cell. **C–D.** Conidia attached to conidiophore with crenate sterile cells. **E.** Conidia. Scale bars: A = 200 μm, C–E = 5 μm.

km ESE of Leibnitz, Rabenhofteiche, ca. 2 km NE of St. Veit am Vogau, on *Carex brizoides*, 15 Apr. 1983, C. Scheuer (GZU 000345111); Styria, Graz, Lustbühel, on *Carex brizoides*, 6 November 1981, C. Scheuer (GZU 000345110); Styria, Spielfeld-Straß, Attemsmoor, on *Carex* sp., 8 Oct. 1986, P. Zwetko (GZU 000345097). **France**, Côte-d'Or, Fauverney, La Chassagne, on *Carex flacca*, 10 May 2019, A. Gardiennet (Alain Gardiennet fungarium AG19067). **Germany**, Brandenburg, Alt Schadow, Krieg, on *Carex acutiformis*, 18 Oct. 1998, V. Kummer (Volker Kummer fungarium VK-P-2553/11); Brandenburg, Alt Schadow, Raatschweg, on *Carex riparia*, 16 Jun. 2018, V. Kummer (Volker Kummer fungarium VK-P-3849/43); Brandenburg, Golßen, Zützen, on *Carex acutiformis*, 23 Oct. 2016, V. Kummer (Volker Kummer fungarium VK-P-4047/24); Brandenburg, Potsdam, Bornim, Pannenberg, on *Carex humilis*, 18 May 2002, V. Kummer (Volker Kummer fungarium VK-P-2529/3).

Notes: The sample identified here as *Ar. cf. sporophleoides* comes from Scheuer (1996), who considered this species a synonym of *Ar. sporophleum*, rejecting the criterion of Petrak (1959) and following the broad concept of Ellis (1965) instead. The sample analysed in the present work has fusoid conidia that resemble those of *Ar. sporophleum*, but the latter are wider, (5–) 6–8(–9) μm , vs. 5–5.5 μm in *Ar. cf. sporophleoides*. This subtle difference was the only useful diagnostic feature found between both clades, but additional samples are needed to confirm its utility.

Key to species of *Arthrinium* s. str.

- | | |
|---|---------------------------|
| 1. Conidia navicular, fusiform or limoniform | 2 |
| 1. Conidia differently shaped | 6 |
| 2. Conidia fusiform < 30 μm long | 3 |
| 2. Conidia navicular > 30 μm long | 5 |
| 3. Conidia < 15 μm long | 4 |
| 3. Conidia 15–25 μm long | <i>Ar. ushuvaiense</i> |
| 4. Conidia < 6 μm wide | <i>Ar. sporophleoides</i> |
| 4. Conidia 5–8.5 μm wide | <i>Ar. sporophleum</i> |
| 5. Conidia > 15 μm wide | <i>Ar. japonicum</i> |
| 5. Conidia < 15 μm wide | <i>Ar. caricicola</i> |
| 6. Conidia curved | 7 |
| 6. Conidia differently shaped | 11 |
| 7. Conidia with rounded ends | 8 |
| 7. Conidia with horned ends | 9 |
| 8. Conidia < 15 μm long | <i>Ar. curvatum</i> |
| 8. Conidia > 20 μm long | <i>Ar. kamschaticum</i> |
| 9. Conidia with horns curved inwards | <i>Ar. luzulae</i> |
| 9. Conidia with horns curved outwards | 10 |
| 10. Conidia > 20 μm long | <i>Ar. cuspidatum</i> |
| 10. Conidia < 20 μm long | <i>Ar. muelleri</i> |
| 11. Conidia globose to ovoid | 12 |
| 11. Conidia angular | 14 |
| 12. Conidia ovoid or broadly ellipsoidal | <i>Ar. lobatum</i> |
| 12. Conidia globose | 13 |
| 13. Conidia 7.5–9.5 μm diam., with a colourless dome-shaped wall section | <i>Ar. globosum</i> |
| 13. Conidia 6–8 μm diam | <i>Ar. sphaerospermum</i> |
| 14. Conidia polygonal | <i>Ar. puccinioides</i> |
| 14. Conidia irregularly angular | 15 |
| 15. Conidia crenate in face view | <i>Ar. crenatum</i> |
| 15. Conidia not crenate in face view | 16 |

16. Sterile cells with long lateral projections *Ar. fuckelii*
 16. Sterile cells lacking lateral projections 17
17. Conidia irregularly rectangular with concentric rings *Ar. austriacum*
 17. Conidia oblong or irregular in face view *Ar. morthieri*

DISCUSSION

In the present study, genetic, morphological and ecological differences between *Apiospora* and *Arthrinium* are considered sufficient to support the taxonomic separation of the two genera. Smith *et al.* (2003) were apparently the first to compare 28S nrDNA data from *Apiospora* sexual morphs and “*Papularia*”-like *Arthrinium* asexual morphs, and found them to form a monophyletic clade. Crous & Groenewald (2013) confirmed these results with a much-improved dataset including additional genetic markers and species, and considered both genera synonyms. *Nigrospora* was later shown to be the most closely related genus within *Apiosporaceae* by Wang *et al.* (2017), in agreement with previous morphological studies that highlighted the similarities between *Nigrospora* and its sexual morph *Khuskia* (Hudson 1963b) with the “*Papularia*”-like species of *Arthrinium* and *Apiospora* (Minter 1985, Eriksson & Hawksworth 1993). However, genetic differences between the “*Papularia*”-like species of *Arthrinium* that grow worldwide mainly on *Poaceae*, and some species found on *Cyperaceae* and *Juncaceae* in temperate or cold habitats (*Ar. puccinioides*, *Ar. japonicum*) could already be observed in the phylogenetic analyses conducted by Singh *et al.* (2012), Sharma *et al.* (2014), Wang *et al.* (2018), and Yan *et al.* (2019), although the issue was not discussed by these authors or investigated further. Pintos *et al.* (2019) analysed the type species of *Arthrinium*, *Ar. caricicola*, and found that it groups with the samples occurring mainly on *Cyperaceae* and *Juncaceae* hosts in temperate or cold habitats, suggesting that this clade is not monophyletic with *Apiospora* and the “*Papularia*”-like species of *Arthrinium*.

The analysis of additional collections of *Arthrinium* associated with *Cyperaceae* and *Juncaceae* (and rarely *Poaceae*) found in temperate or cold habitats revealed that they are also related with *Ar. caricicola* within *Arthrinium s. str.* Phylogenetic inference suggests that this clade is not monophyletic with the one containing basauxic species occurring worldwide (also in tropical and subtropical habitats) mainly in *Poaceae* hosts, which are here combined to *Apiospora*. However, the host plants associated to *Arthrinium* and *Apiospora* seem to be diverse, especially for *Apiospora*, so they cannot be employed as a perfect diagnostic feature to discriminate both genera. For example, *Ap. pterosperma* has been found thus far, exclusively associated with *Cyperaceae* plants (genera *Machaerina* and *Lepidosperma*), and other species of *Apiospora* have been occasionally reported too in *Carex* or *Juncus* (e.g. *Ar. phaeospermum sensu* Ellis 1965, but these records need to be confirmed). On the other hand, samples of *Ar. crenatum*, *Ar. curvatum* and *Ar. puccinioides* have been found on *Poaceae*. Regarding the climate, all sequenced collections of *Arthrinium s. str.* come from temperate, cold or alpine climates. A few of them, such as *Ar. cuspidatum*, *Ar. fuckelii* or *Ar. luzulae*, occur in alpine habitats and snowbanks (Minter & Cannon 2018), and could be considered psychrophiles. Presently the only sequenced records of *Arthrinium s. str.* in Asia are those of *Ar. japonicum*, found in the northernmost part of Honshu island

(Japan) in a cold climate, as well as a sequence obtained from soil samples (KT265189, Hu *et al.* 2014) found at 4 800 m asl in the Tibet Plateau (China). Verified records of *Arthrinium s. str.* from tropical or subtropical habitats are lacking, suggesting that this genus could be absent from areas subjected to these climates.

On the contrary, *Apiospora* seems to be a cosmopolitan genus present in tropical, subtropical, temperate and cold climates. The type species, *Ap. montagnei*, was found on *Poaceae* hosts (*Arundo*, *Piptatherum*) not known for any species of *Arthrinium* or *Nigrospora*. The original samples were collected in Mediterranean lowlands (Perpignan, Algiers) where *Arthrinium s. str.* species have not been found. In the present work, a lectotype of *S. apiospora* (\equiv *Ap. montagnei*) has been selected among the original collections stored at PC (Paris, France) as a first step to fix the identity of this species. A sample collected near Perpignan on *Arundo* sp. was chosen because of its good conservation status, and also because these are the first locality and plant host mentioned in the protologue. With this choice, *Ap. marii* and *Ap. phragmitis* are the most probable synonyms of *Ap. montagnei*, but additional samples obtained near the type locality are needed to confirm if other species of *Apiospora* occur on the putative host plant species (*Arundo micrantha* or *A. donaciformis*) and select an epitype with a known genetic profile.

The phylogenetic placement of other putative species of *Arthrinium s. str.* still needs to be resolved. Some of these are likely synonyms of earlier taxa on the basis of their morphological similarities (e.g., *Ar. naviculare* and *Ar. carinatum* = *Ar. caricicola*, *Ar. bicorne* and *Ar. juncoideum* = *Ar. cuspidatum* Cooke 1954). However, there could be other scenarios. For example, results obtained in the present study suggest that *Ar. sporophleum* and *Ar. sporophleoides* are distinct species with just slight morphological differences, while other names could also hide cryptic species (e.g. *Ar. puccinioides*). Therefore, putative synonymies with old names need to be reconfirmed with type studies, extensive sampling and genetic analyses. Information from other putatively distinct species of *Arthrinium s. str.* is also missing. *Arthrinium kamtschaticum* (first found in *Carex* sp. in Kamchatka, eastern Russia), has curved conidia resembling those of *Ar. curvatum*, but darker and larger (22–32 × 10–14 µm in *Ar. kamtschaticum* vs. 11–15 × 6–8 µm in *Ar. curvatum*) (Pollack & Benjamin 1969). *Arthrinium cuspidatum*, a species associated with *Scirpus* (*Cyperaceae*) and *Juncus* (*Juncaceae*) seems to occur in alpine areas of Europe (Suková *et al.* 2003) and the USA (Cooke 1954). It has lunulate conidia resembling those of *Ar. luzulae*, but in the first species the edges are pointing outwards, while in the latter they point inwards. Due to its habitat and morphological features, *Ar. cuspidatum* could be a genuine species of *Arthrinium s. str.* *Arthrinium muelleri* has curved conidia, 15–20 × 8–10 µm that sometimes point outwards, recalling those of *Ar. cuspidatum* (15–19 × 7–14 µm, Minter & Cannon 2018). It has been found in alpine areas of

Switzerland (Ellis 1976) and Austria (Scheuer 1996), growing on *Carex*. *Arthrinium fuckelii* resembles *Ar. morthieri* because both species grow on *Carex* and have quadrangular conidia, but those of *Ar. morthieri* are smaller (11–16 × 11–16 × 5–9 µm vs. 7–9 × 16–19 × 3.5–5 µm in *Ar. fuckelii*, Gjørnum 1967, Minter & Cannon 2018), and *Ar. fuckelii* has sterile cells lacking lateral projections (present in *Ar. fuckelii*). *Arthrinium globosum* has globose conidia similar to those of *Ar. sphaerospermum*, but they are larger (9 × 8 µm vs. 7 × 6 µm in *Ar. sphaerospermum*) and have a well-defined hyaline dome-shaped wall (Koskela 1983). *Arthrinium* s. str. might also include *Ar. ushuvaiense*, a taxon with lobate sterile cells and navicular conidia similar to those present in *Ar. japonicum*. It was found growing on *Luzula* (*Juncaceae*) in Tierra del Fuego (Argentina) (Spegazzini 1887, Gjørnum 1967, Ellis 1971). Finally, *Ar. lobatum* was found in alpine areas of Venezuela. It has also lobate sterile cells but presents ovoid conidia. Despite the effect of altitude, this would be the first species of *Arthrinium* known to occur in a tropical region, so it needs to be confirmed.

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Supplementary Table S1. GenBank accession numbers and isolates employed in the phylogenetic analyses. Names in bold represent samples sequenced for the present study.