Circumscription and typification of sphagnicolous omphalinoid species of *Arrhenia* (*Hygrophoraceae*) in Newfoundland and Labrador: three obligate and one facultative species

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**Abstract**

Molecular studies of sphagnicolous arrhenias in Newfoundland and Labrador (NL) revealed four clades in *Arrhenia*, three obligate (two scaly capped and one smooth-capped) and one facultative (smooth-capped) sphagnophiles. Critical nomenclatural review of 16 names used for omphalinoid sphagnicolous taxa in the past left five suitable to apply to this group. One scaly capped obligate sphagnophilic clade contained the type for *Arr. gerardiana* and the other, the type for *Clitocybe gerardiana* var. *fusca*; the latter we introduce as the novel species *Arr. bigelowii*. It differed from the first by longer spores and a darkening reaction in 10% of collections. The smooth-capped third obligate sphagnophilic clade contained the types of *Agaricus telmatiaceus* and *Omphalina fusconigra*; we recombined it as *Arr. telmatiaceae*. This is the darkest species of the group, with a more northern distribution in NL. The facultative sphagnophile was identified as *Arr. philonotis*, a lighter smooth-capped species also with a more northern distribution in NL. Unexpectedly, we also collected an unidentified smooth-capped facultatively sphagnophilic species of *Omphalina* of the *O. pyxidata* complex. All five species are distributed in both Europe and North America. We describe each species of *Arrhenia* with a sequenced type, providing new type material where needed. Overall, this study adds new sequences from over 80 specimens of sphagnicolous arrhenias to the two existing in GenBank when we began in 2006, 11 new sequences of the unidentified species of *Omphalina*, and several other arrhenias.

**Keywords**  *Arrhenia oniscus* · *Arrhenia sphagnicola* · *Omphalina rivulicola* · Bog agarics · Bog *Arrhenia* · New taxon · New combination

**Introduction**

*Arrhenia* was erected as a genus by Fries (1849), and belongs to the *Hygrophoraceae* (Lodge et al. 2014). As circumscribed by Redhead et al. (2002), it contains species with basidiomata varying from pleurotelloid to omphalinoid, pilei varying from nutant to infundibuliform, hymenia varying from reduced (flat, wavy, wrinkled or folded) to gilled, and stipes varying from absent, reduced, or rudimentary, to fully developed, placed laterally, eccentrically, or centrally, all particularly well represented in arctoalpine habitats. Agaric species with small basiomata having an umbilicate pileus, decurrent gills and central stipe have been described as omphalinoid, although many are not in the genus *Omphalina*, including many arrhenias. MycoBank ([mycobank.org](http://mycobank.org)), accessioned 18 Mar 2022) lists over 80 valid species names, a number that is bound to change with more study, as...
some may become synonymized, while others may turn out to hide complexes of similar taxa. Common traits for most members of the genus include small size, brown-grey colour, preference for open areas, and bryophilia.

In this study we consider only taxa found with *Sphagnum* L., and use the term obligate sphagnophile for those not found separately from *Sphagnum*, and facultative sphagnophile for those found in *Sphagnum* with some regularity, but also among other mosses, usually in barren locations where *Sphagnum* is present. Our definition excludes species normally preferring other habitats, even if found on occasion in *Sphagnum*, presumably by chance (e.g. an occasional *Craterellus* Pers., or a lignicolous species on wood that happens to be in *Sphagnum*). Our interest to learn more about this group in the Canadian province of Newfoundland and Labrador (NL) was stimulated in part because over 15 years one of these species has been the logo for Foray Newfoundland and Labrador (FNL), the mushroom club of the province, with which three of the four authors are or have been associated.

**History of nomenclatural usage**

Earlier treatments of species we now consider omphalinoid sphagnicolous arrhenias applied epithets inconsistently, using several names for what seems like a small number of taxa. Increasing consistency in both morphologic species concepts and nomenclature began to emerge during the last 75 years. Eleven major publications by 12 authors who have collected and studied these species (i.e. excluding check lists and general reviews or descriptions of regional mycota), use eight names between them to describe three to four different morphospecies: Favre (1948)—3; Redhead (1979)—2; Clémençon (1982)—4; Lange and Lange (1982)—2; Bigelow (1958, 1985)—5; Kuyper (1995)—3; Breitenbach and Kränzlin (1991)—2; Bon (1997)—4; Gminder (2001)—1; and Elborne (2012)—3. Undoubtedly Jules Favre, father of alpine mycology and mycoecology (Brunner et al. 2017), provided the pivot point to a more coherent and unified taxonomy and nomenclature of sphagnicolous arrhenias. Regular collecting in montane bogs (Favre 1948) gave him unsurpassed familiarity with these species in their environment. Seven seasons of daily collecting trips to the alpine zone of the Swiss National Park (Favre 1955) widened his command of the omphalinoid group of exposed heathland, making his work the cynosure for this mycota, inspiring and influencing subsequent investigators for a long time. With the obvious expertise of his factual observations came occasional nomenclatural conventions based on less accurate influences. These in no way lessened the enormous contribution of Favre, but did propagate some nomenclatural problems in this small group. Below we review names used for omphalinoid sphagnicolous arrhenias by year of publication, taken from the above ten major publications or their authors, as well as names, synonyms, and citations found in the pertinent protologues—adding a few from diverse sources—and assess the suitability of each to sphagnicolous arrhenias.

**Review of nomenclature**

1. 1782. *Agaricus tigrinus* Bull., nom. sanct. Described as a white, lignicolous species (Buillard 1782) and later recombined by Fries (1818) as *Lentinus tigrinus* (Bull.) Fr., nom. sanct., the name by which we know it today. This white wood dweller does not fit a grey-brown, sphagnicolous *Arrhenia*, and was not considered a sphagnicolous *Arrhenia* by author or sanctioner. It is listed here because taxonomic confusion has caused some of its homo- and synonyms to be so considered.

2. 1794. *Agaricus epichysium* Pers., nom. sanct. Described as growing on hollow willow trunks (Persoon 1794), this species is currently known as the wood-dwelling *Arrhenia epichysium* (Pers.) Redhead, Lutzoni, Moncalvo & Vilgalys. Because rotten wood can also be found in bogs, lignicolous fungi have been collected from *Sphagnum* (Bunyard et al. 2008). Possibly because of such chance association the name “epichysium” has been applied to some of these species on occasion, persisting as late as 1982 (Lange and Lange 1982). Currently *Arr. epichysium* is not considered a sphagnicolous species and we do not consider the name suitable for sphagnicolous arrhenias.

3. 1801. *Agaricus epichysium* var. *icmadophilus* Pers., nom. sanct. In translation, Persoon’s (1801) entire description, omitting measurements, reads: “very delicate, pileus funnel-shaped and dark grey, gills plano-decurrent and grey. Arising in turf among *Sphagnum*.” Initially Bigelow (1958) preferred this laconian description, sanctioned by Fries (1821), over the use of the light-coloured “oniscus” for the dark sphagnicolous *Arrhenia* species, and transferred it to *Clitocybe*, raising it to species level. Later Bigelow (1985) gave up *icmadophilus* in favour of *oniscus*, because he felt that the description of *Ag. epichysium* var. *icmadophilus* lacked specific identifying features, and “is very short and could also be of several species”. In his doctoral thesis, Redhead (1979) followed Bigelow, but states (personal communication, 2018) that by 2002 he had “acquiesced to standard usage”. Apart from these brief but transient uses, the epithet has never been in common usage and has not been applied to this group. We find nothing convincing in the scant protologue of *A. epichysium* var. *icmadophilus* that compels us to apply the name to any species of sphagnicolous *Arrhenia* with conviction, and in view of the absence of type material, paucity of detail in the protologue, and lack of
continued usage, we are content to follow Bigelow and Redhead in this matter.

4. 1805. “Agaricus tigrinus Alb. & Schw.” Fries (1818, 1821) cites these authors’ publication while describing Agaricus affricatus Fr. This may have confused some workers into thinking the description of Ag. tigrinus by von Albertini and von Schweinicz (1805) is the protologue for a new species, something claimed by neither Fries nor von Albertini & von Schweinicz. The latter’s Conspectus is a treatment of regional mycota, made up of both new and previously known species. They mark all new species “nobis” (Latin for “from or by us”, in the sense of described as new by us) and provide a list of the new species they describe (Catalogus fungorum novorum nostrantium, p XIII). Agaricus tigrinus is not marked “nobis” and does not appear in the list, making it clear that von Albertini & von Schweinicz did not introduce it as a new species. The title of their book states “e metodo Persooniana” to indicate that they refer to Persoon’s work. Thus, in this case, they refer to Persoon’s 1801 description of Agaricus tigrinus. In turn, Persoon also did not proffer his description as that of a new species, but cites earlier descriptions by Sowerby and by Bulliard. With the latter citation we have come full circle to the first taxon in this list, indicating why it needed to be included. “Agaricus tigrinus Alb. & Schw.” does not exist and cannot be used.

5. 1818. Agaricus affricatus Fr., nom. sanct. This epithet is occasionally (mis)applied to sphagnicolous arrhenias, probably because Fries (1818) described it as common in swamps (copiose in paludibus). No doubt the description of an omphalinoid agaric in swamps, with darkening (nigrantibus), grey, bristly scales (squamulis pilosis), and deeply decurrent, whitish, subdistant gills. He described the cap as sallow (lurido), light grey (subcinereus), and sparsely woolly (leviter tomentosus). Qualifiers in formal descriptions are used to distinguish the character qualified from its “normal” state; of the two, the qualifier becomes the more important descriptor. If Lasch felt it necessary to add “leviter”, it was to stress the sparse nature of the cap ornamentation, to distinguish it from species with truly tomentose caps. Even should one consider “leviter” a relative concept, and dismiss “lighty, slightly, sparsely” or “minutely” as subjective, there should be no misunderstanding the meaning of “tomentosus”. The term is specifically used to indicate woolly, fuzzy, fine hair, and not scales; the latter would require terms like “scabrosus” or “squamosus”. Lasch’s description of Ag. philonotis is compatible with smooth-capped sphagnicolous arrhenias.

6. 1818. Agaricus incomitus Fr., nom. sanct. Described as sphagnicolous by Fries (1818), but to our knowledge, hitherto not applied to a species of Arrhenia. Fries described the cap and stem as grey and the gills as dirty white, yellowing with time. Unlike our sphagnicolous arrhenias, the gills are adnate, not decurrent. Fries also cited varieties rimosa and truncigena of Agaricus discolor, as described by von Albertini & von Schweinicz. These authors described the former as a woodland species and the latter as lignicolous, reinforcing that this epithet, possibly encompassing several current taxa, is not applicable to sphagnicolous species of Arrhenia.

7. 1818. Agaricus oniscus Fr., nom. sanct. Both in his protologue (Fries 1818) and sanctioning description (Fries 1821) of this species, Fries leaves no doubt that he is providing a new name for Ag. cespitosus Bolton (1788). A recent review (Voitk 2022) of the protologues and associated original material of both determined that Ag. cespitosus was a later synonym for the species currently known as Lichenomphalia umbellifera, and because Fries had declared Ag. oniscus a synonym for Ag. cespitosus, Ag. oniscus also becomes a later synonym for that taxon. The name, therefore, is both unsuitable and unavailable for sphagnicolous arrhenias.

8. 1828. Agaricus philonotis Lasch. Lasch (1828) described this species, currently known as Arrhenia philonotis (Lasch) Redhead et al., from bogs near Brandenburg, a basidioma with an umbilicate cap and deeply decurrent, whitish, subdistant gills. He described the cap as sallow (lurido), light grey (subcinereus), and sparsely woolly (leviter tomentosus). Qualifiers in formal descriptions are used to distinguish the character qualified from its “normal” state; of the two, the qualifier becomes the more important descriptor. If Lasch felt it necessary to add “leviter”, it was to stress the sparse nature of the cap ornamentation, to distinguish it from species with truly tomentose caps. Even should one consider “leviter” a relative concept, and dismiss “lighty, slightly, sparsely” or “minutely” as subjective, there should be no misunderstanding the meaning of “tomentosus”. The term is specifically used to indicate woolly, fuzzy, fine hair, and not scales; the latter would require terms like “scabrosus” or “squamosus”. Lasch’s description of Ag. philonotis is compatible with smooth-capped sphagnicolous arrhenias.

9. 1836. Agaricus sphagnicola Berk. The use of this name for sphagnicolous arrhenias has been very confusing. Because Berkeley (1836) described the cap of Ag. sphagnicola as “minutely squamulose”, many workers have applied the epithet to scaly capped sphagnicolous arrhenias, while others, like Redhead (1979) in his original report, and Kuyper (1995) found that Berkeley’s description, according to Kuyper, “seems to fit better for Phytoconis ericetorum” (= L. umbellifera). A recent detailed analysis of Berkeley’s protologue (Voitk 2022) supported the early opinion of Redhead (1979), and agreed with Kuyper (1995) that Berkeley’s protologue fit with L. umbellifera, but produced significant conflicts, if applied to sphagnicolous arrhenias. For
nomenclatural stability, the species was neotypified with a specimen collected and identified by Berkeley as *Ag. sphagnicola*, and subsequently identified by Redhead (1979) as *Geronema ericetorum* (= *L. umbellifera*), making this unsuitable name unavailable for sphagnicolous arrenhias.

10. 1865. “*Agaricus affricatus* Berk. & Broome”. Berkeley and Broome (1865) applied *Ag. affricatus* Fr. (see beginning of this list) to a different species by mistake. Because the name was already in use within that genus, its use for another species was illegitimate, making it unavailable for sphagnicolous arrenhias.

11. 1873. *Agaricus gerardianus* Peck. Along with a coloured aquarelle, Peck (1873) described a small, brown mushroom with a cap that was “rough with scattered blackish points”, growing in “sphagnous marshes” of New York State. This is the first unambiguous description of a truly scaly capped sphagnicolous omphaloid species, clearly shown on the illustration. In the margin of his early hand-written notes Peck wrote, “Is it *Ag. affricatus*,” indicating that he actively considered earlier and equally scaly descriptions, before concluding that this was a new species. It has been transferred to *Arrhenia* (Elborne 2008), and is currently known as *Arrhenia gerardiana* (Peck) Elborne. The description fits scaly capped sphagnicolous arrenhias.

12. 1883. *Agaricus telmaticus* Berk. & Cooke. This name appeared with the reproduction of an aquarelle by George Massee of his collection near Scarborough, in volume 2 of Cooke’s “Illustrations of British Fungi (*Hymenomycetes*)” (Cooke 1881–1883). The Illustrations appeared in installments, and *Ag. telmaticus*, plate 240, appeared Apr.–May, 1883 (Stafleu and Cowan 1976). In addition to illustrating the taxon, Massee’s watercolour contained separate analytic figures (figures in addition to those illustrating the species generally, demonstrating details to aid identification), e.g. depictions of spores, gill shape, tiers of lamellulae, stem context and content, etc. The “Handbook of British Fungi, Second and revised edition” (Cooke 1883–1891), for which the Illustrations were meant to be an atlas, also appeared in parts; the segment treating *Ag. telmaticus* appeared Jan.–Apr., 1885 (Stafleu and Cowan 1976). Although the synopsis appeared 2 years after the name, the name was valid on publication, because the International Code of Nomenclature for algae, fungi, and plants (henceforth the Code; Turland et al. 2018) accepts an illustration and figure with analysis in lieu of a synopsis for taxa published before 1908. Berkeley & Cooke cited Cooke’s 1871 treatment of *Ag. affricatus* Berk. & Broome, to indicate this was the same species, but because they provided a new name, a new synopsis, a new illustration, and a new type specimen, they made it clear that they were publishing the new name as a new species, not a replacement name for the old type specimen. That this was their intent is confirmed by an annotation, “Type”, on the herbarium sheet of Massee’s collection from Scarborough, and “from type” on Massee’s aquarelle depicting the same collection. Dennis (1948) reviewed *Ag. telmaticus* and noted the confusion of names, authors, collections, and illustrations. He concluded that Massee’s collection from Scarborough was the type specimen for *Ag. telmaticus*. The description of this taxon is compatible with a dark smooth-capped sphagnicolous species of *Arrhenia*.

13. 1883. *Agaricus peculiaris* Britzelm. Apart from giving a fitting size, the entirety of Britzelmayr’s (1883) very sparse protologue is that his new bog species has grey, moderately spaced gills with spores 11–14 × 4 μm, and is near *Ag. oniscus*. He does not state whether the cap is umbilicate or plane, smooth or scaly, or whether the gills are decurrent or adnate. An illustration shows a grey-black mushroom with a smooth, black-brown, deeply infundibuliform cap with decurrent gills. Comparison of other known scaly capped species illustrated by Britzelmayr showed that he illustrated scaly caps faithfully, confirming that he is describing a smooth-capped
species. Illustrated spores are doubly curved with a Q value 3.4–4.5 (average 3.8). None of our smooth-capped sphagnicolous arrheniads has spores even close to this size; only one scaly capped species has spores in this length, but not as prominently doubly curved and with and average Q of 2.3, and no Q value above 3.3. The image does not fit with any of our species either macroscopically or microscopically. Bresinsky and Strangl (1974), in an effort to redfine taxa described by Britzelmayr, explored the type locality, and identified what they believed to be the same species as *Omphalina sphagnicola* (Berk.) M.M. Moser, based on comparison with a non-type collection by Britzelmayr, made 15 years after the protologue. Bresinsky & Stangl provide no descriptive information about either specimen. Unable to fit the original material to sphagnicolous *Omphalina* we shall not consider this name here.

15. 1958. *Clitocybe gerardiana* var. *fusca* H.E. Bigelow. The effort to consider white-spored fungi with funnel-shaped caps as members of *Clitocybe* presented Bigelow an opportunity to review several species of *Omphalina*, including many that have since been transferred to *Arrhenia*. On reassigning Peck’s *Agaricus gerardianus* to *Clitocybe*, Bigelow encountered some darker specimens, seemingly limited to a small locality, microscopically indistinguishable from the more widespread lighter specimens. In a later review of *Clitocybe* Bigelow (1985) states that he first described this entity as *Clitocybe sphagnorum* Bigelow, “nom. prov.”, in his PhD dissertation. However, when he came to describe it formally he decided it was more aptly ranked as a variety, and named it *Clitocybe gerardiana* var. *fusca* Bigelow (Bigelow 1958). He described it as a scaly capped sphagnicolous species with dark caps, squamulose in the middle and smooth at the periphery. After publication of the variety, he became misled to believe that it was the same entity as *Omphalina fusconigra* P.D. Orton, and synonymized his variety with Orton’s species (Bigelow 1985). Bigelow’s description remains suitable for scaly capped sphagnicolous arrheniads.

16. 1960. *Omphalina fusconigra* P.D. Orton. Orton (1960) was unable to find an existing “description which fit this rather characteristic sphagnicolous agaric”, which differed “from the other sphagnicolous species of *Omphalina* in consistently darker blackish brown cap and stem…” To Orton the main macroscopic character worthy of note, which readily distinguishes this species from other sphagnicolous arrheniads, is the dark, black-brown colouring, not cap texture. He described the cap as “sometimes slightly rugulose or scurfy-floculose at centre”, in other words an irregularity that was the exception, minimal, and limited. Both wrinkled (rugulose) and flat surfaces can be scaly, scurfy-floculose, or smooth. Probably because scaly capped arrheniads are commonly encountered in bogs, the mention of any cap irregularity, no matter how uncommon, limited or inconsequential, tempted misinterpretation of *O. fusconigra* as a scaly capped taxon. For example, that is probably what led Bigelow (1985) to synonymize his scaly *Clitocybe gerardiana* var. *fusca* with Orton’s dark but smooth-capped *Omphalina fusconigra*. We conclude that this name, currently *Arrhenia fusconigra* (P.D. Orton) P.A. Moreau & Courtec., is suitable to apply to dark smooth-capped sphagnicolous arrheniads.

In summary, from a field of 16 potential candidates, we identified five epithets that fit the species we have observed in our bogs, two with clearly scaly caps (*Ag. gerardianus*, and *C. gerardiana* var. *fusca*) and three with primarily smooth caps, albeit keen observation may reveal some irregularity or fine surface ornamentation at times (*Ag. philonotis*, *Ag. telmatiaeus*, and *O. fusconigra*).

**Materials and methods**

Type collections Peck (1873) listed two collections in his protologue of *Ag. gerardianus*, but did not specify either as type; only one of the two syntypes could be located. All four basidiomata (NYSf 1339.1–4) of this collection were examined, but their condition was not sufficiently robust to permit sequencing. Two attempts to find fresh collections around the type locality near Sand Lake, NY, were unsuccessful, so that one of Peck’s contemporaneous collections from Essex Co., NY, identified by him as *Ag. gerardianus*, was selected (NYSd 4725). One basidoma (NYSd 4725.1) from this was used for both DNA extraction and microscopy. The spore size of NYSd 4725.1 matched that of all four basidiomata in Peck’s syntype, NYSf 1339.1–4. The type collection for *Clitocybe gerardiana* var. *fusca*, collected by A.H. Smith, contains over 30 basidiomata. From that collection, MICH made a gift of a fragment consisting of approximately ½ pileus with gills attached, which was used for both DNA extraction and microscopy. The remaining material from this gift was deposited in TUF (TUF117871). One basidoma from the type collections of *Ag. telmatiaeus* in NY, and one from *O. fusconigra* in K were sequenced successfully.

**Other collections** Study collections were selected from over 150 collections identified to be sphagnicolous omphaloid arrheniads in the private herbaria of Andrus Voitk and FNL, collected with normal field techniques and air-dried at 20–30 °C. Selection attempted to incorporate samples of all potential “species” and to represent a wide distribution in NL. In
addition, nine collections from an archipelago near Saint-Augustin, Québec, on the north shore of the St Lawrence Basin, a similar area contiguous with the southern Labrador coast, were included. Specimens not associated with Sphagnum were included if Sphagnum was nearby and collections of similar sphagnicolous specimens had been made. Three collections from mossy grassland with no nearby Sphagnum were added to compare to similar specimens collected in Sphagnum.

Of 64 selected regional collections, sequences were obtained from 60. Two were excluded after analysis because they were unidentified singleton species from a distant portion of the Arrhenia tree for which we had no photo and inadequate habitat or substrate data, leaving 58 sequenced collections, which make up the core regional target material for this study (51 from NL, seven from QC; 36 from Voitk, 22 from FNL). In addition, 35 extraregional collections of sphagnicolous arrhenias from various herbaria were sequenced for this study, to which were added two GenBank sequences of sphagnicolous arrhenias available at the time. Herbaria are designated with Index Herbariorum codes (Thiers 2021). A few additional collections were made, examined, and sequenced after the phylogenetic analysis had been completed; these were not included in the tree, but have been added to the Tables, material deposited as the others.

Macroscopic examination NL specimens were photographed in situ and macroscopic descriptions were based on fresh specimens. Apart from capsule descriptions of types, only personally observed sequence-identified regional specimens were used for taxonomic descriptions.

Microscopic examination Light microscopic observations (Zeiss 392560 with Apo 100/1.25) were conducted at 1000 × magnification (oil immersion), using 2% KOH. Spore length and width were measured to 0.5-μm accuracy; measurements deviating from 0.5-μm increments are due to calculation of an objective correction factor. A minimum of 20 spores per single basidioma was used to calculate average values, and Q (length width ratio) was rounded to one decimal point. Statistical analysis of spore sizes was done with a Student’s t-test (two-tail, two-sample assuming equal variances) using the data analysis package in Microsoft Excel 2013.

DNA extraction and nuclear sequencing DNA extraction and nuclear sequencing were done in three laboratories. Extraction at Bridgewater College (sequences marked with * in Table 1) followed Lickey et al. (2003); extraction at The Field Museum (sequences without a UDB code and not marked with * in Table 1) followed Sulzbacher et al. 2016; extraction at Tartu University (UDB code in Table 1) followed Saar and Voitk (2015). Sequences were inspected and assembled using Sequencher 5.4 software (Gene Codes, Ann Arbor, USA), and uploaded into PlutoF cloud database (Abarenkov et al. 2010b), including the collection data, partly reachable through the public web output UNITE (http://unite.ut.ee; Abarenkov et al. 2010a). Nucleotide sequence data were deposited in GenBank (see Tables 1, 2, and 3).

Phylogenetic analysis The alignments were performed using L-INS-i strategy as implemented in MAFFT v7.475 (Katoh and Standley 2013). Minor manual adjustments were performed with SeaView 4.7 (Gouy et al. 2010). Bayesian inference of phylogeny was performed with MrBayes 3.2.6 (Ronquist et al. 2012) with default values; the first 100K generations without reaching a stable likelihood score were discarded.

Maximum likelihood (ML) analysis was performed with RAXML-HPC BlackBox v.8.2.9 (Stamatakis 2014), at the Cipres Science Gateway (Miller et al. 2010; http://www.phylo.org/). Analyses deposited in TreeBase, http://purl.org/phylo/treebase/phylows/study/TB2:S29346.

Results

The specimens studied are summarized in three tables. Table 1 gives details of collections whose sequences make up the phylogenetic tree in Fig. 1, excluding an unidentified species in the Omphalina pyxidata complex and the sphagnicolous arrhenias. Data for collections of the unidentified species in the Omphalina pyxidata complex examined for this study, whether shown in Fig. 1 or not, are summarized in Table 2, and data for the sphagnicolous arrhenias examined for this study, including those used to make up the phylogenetic trees in Figs. 1 and 2, as well as those added later and not in Fig. 1, are shown in Table 3.

Phylogeny

The studied collections produced two singleton collections (Arrhenia spp. 1 and 2) and four clades within Arrhenia, as well as a monophyletic clade that fell in Omphalina, labeled Omphalina sp. (Figs. 1 and 2). Two scaly capped sphagnicolous species arose as sister clades from the most ancestral lineage in the arm leading to Arrhenia, while the two smooth-capped species emerged later. A more detailed look at these four species (Fig. 2) reveals that the epitype of Ag. gerardianus (NYSd 4725) fell into one scaly capped clade, giving it its name, and Bigelow’s holotype of C. gerardiana var. fusca fell into the other, which we describe as a new species, Arr. bigelowii. Berkeley & Cooke’s holotype for Ag. telmatiaeus and Orton’s holotype for O. fusconigra fell into a clade of dark smooth-capped obligatory sphagnicolous basidiomes, making
O. fusconigra a later synonym of Ag. telmatiaeus. We transfer the latter to Arrhenia as Arr. telmatiaeus (Berk. & Cooke) Voitk & I. Saar, comb. nov. The remaining clade we identify as Arr. philonotis, and declare a neotype from Germany for the species. Two singleton specimens, labeled Arrhenia sp. 1 and Arrhenia sp. 2 on Fig. 1, fell elsewhere within Arrhenia. They were initially identified as “Arrhenia sphagnicola”, a name primarily, but not exclusively, used for scaly capped sphagnicolous arrhenias at the time; because we have very little tissue left, lack notes or photographs for these collections, including whether both were sphagnicolous or scaly, and have not collected them again on several return trips to the same sites, we do not treat them here.

### Table 1

| Species (as recorded on GenBank deposit) | GB code above, UNITE code below | Primary Herbarium number above, copy below | Country (province for Canada) | Reference |
|-----------------------------------------|---------------------------------|-------------------------------------------|-----------------------------|-----------|
| Omphalina rivulicola                    | U66451                          |                                           |                             | Lutzoni 1997 |
| Omphalina pyxidata                      | U66450                          |                                           |                             | Lutzoni 1997 |
| Omphalina pyxidata                      | UDB0799020                      | TUF114379                                  | Estonia                     | This study |
| Omphalina cl. rivulicola                | HQ445617                        |                                           | Svalbard                    | Bjørnbeke et al. 2010 |
| Omphalina cl. rivulicola                | GU234117                        |                                           | Svalbard                    | Geml et al. 2012 |
| Omphalina chionophylla                  | GU234114                        |                                           | Svalbard                    | Geml et al. 2012 |
| Omphalina chionophylla                  | MH862276                        |                                           | Svalbard                    | Vu et al. 2019 |
| Arrhenia epichysium                     | KC237880                        | LE262961                                   | Russia                      | Zvyagina et al. 2015 |
| Arrhenia epichysium                     | U66442                          |                                           |                             | Lutzoni 1997 |
| Arrhenia sp. 1                          | ON113349                        | DAOM984939                                 | Canada, NL                  | This study |
| Arrhenia velutipes                      | UDB034634                       | TUF117593                                  | Canada, NL                  | This study |
| Arrhenia philonotis                     | UDB024403                       | M-0155052                                  | Germany                     | This study |
| Arrhenia sp. 2                          | ON113350                        | DAOM984940                                 | Canada, NL                  | This study |
| Arrhenia obscurata                      | MT967333                        | TUF117230                                  | Canada, NL                  | Voitk et al. 2020 |
| Arrhenia obscurata                      | UDB024573                       |                                           |                             | Voitk et al. 2020 |
| Arrenhia acerosa                        | MT967312                        | UPS-F151993                                | Sweden                      | Voitk et al. 2020 |
| Arrenhia svalbardensis                  | MT967358                        | O-50446                                    | Svalbard                    | Voitk et al. 2020 |
| Arrenhia auriscalpium                   | UDB034589                       |                                           |                             | Voitk et al. 2020 |
| Arrenhia auriscalpium                   | U66428                          |                                           |                             | Lutzoni 1997 |
| Arrenhia elegans                        | JF908757                        | MCVE-16455                                 | Italy                       | Osmundson et al. 2013 |
| Arrenhia subglobispora                  | KR606032                        |                                           | Switzerland                 | Senn-Irlet, direct submission (2015) |
| Arrenhia retiruga                       | MT967340                        | TUF117227                                  | Estonia                     | Voitk et al. 2020 |
| Arrenhia retiruga                       | UDB036702                       | O-21925                                    | Norway                      | Sequeced as part of the NorBOL project; no associated publication |
| Arrenhia lobata                         | MT967332                        | DAOM981256 TUF117633                       | Canada, NL                  | Voitk et al. 2020 |
| Arrenhia lobata                         | U66429                          | Lutzoni & Lamoure 910824-1, DUEK            | France                      | Lutzoni 1997 |
| Arrenhia sp.                            | UDB033848                       | DAOM984941 TUF117659                       | Canada, NL                  | This study (later sequence, not in tree) |

### Macromorphology

Phylogenetic clades correlated with morphological characters. Arrhenia bigelowii and Arr. gerardiana, both in the earlier diverging lineage, have pilei usually under 20 mm in diameter, covered to various degrees by radially arranged darkening scales with upturned tips (Figs. 3a–c and 4a–e). Macroscopically the upturned scale tips make distinction between scaly and smooth-capped specimens easy in vivo, but the difference is not readily apparent after drying because often the upturned tips are not obvious microscopically even after rehydration. About 10% or less of the variably brownish Arr. bigelowii specimens undergo a marked darkening reaction (Fig. 4b, d); the species as a whole is a little darker than...
### Table 2  Specimens of the single NL species in the *Omphalina pyxidata* complex\(^{ab}\)

| CODE: GenBank above, UNITE below | Country, state/province, Town, locality above, Coordinates (degree decimal); elevation (m asl) below | Habitat | Substrate | Date DD-Mon-YY | Collector above | Collection code below | Herbarium code: Main above, copy below |
|----------------------------------|-------------------------------------------------------------------------------------------------|--------|-----------|---------------|----------------|----------------------|---------------------------------------|
| MH237678 c                       | CANADA, NL, Pasadena, Pasadena Ski Club, clubhouse lawn 48.984177N, 57.580194W; 171            | grassland | moss      | 24-Sep-13     | Henry Mann    | 13.09.24.av03        | DAOM744407 TUF117362                  |
| UDB032178                        |                                                                                                 |         |           |               |                |                      |                                       |
| MH569861 d                       | CANADA, NL, Flowers Cove 51.288142N, 56.740856W; 1                                           | grass   | moss      | 21-Sep-12     | Andrus Voitk  | 12.09.21.av01        | n/a \(^e\)                           |
| JF908501 f                       | ITALY                                                                                           |         |           |               |                |                      |                                       |
| MH237679 c                       | CANADA, NL, Pasadena, Pasadena Ski Club, clubhouse lawn 48.984177N, 57.580194W; 171            | grassland | moss      | 14-Oct-07     | Henry Mann    | 14.10.07.av01        | DAOM744408 TUF117363                  |
| UDB032179                        |                                                                                                 |         |           |               |                |                      |                                       |
| MH473375g                        | CANADA, NL, Labrador, Forteau, Overfall Brook trail 51.454297N, 56.947339W; 51                    | heath   | *Sphagnum & moss* | 08-Sep-05     | Andrus Voitk  | 05.09.08.av03        | DAOM744411                           |
| MH473374g                        | CANADA, NL, Searston Provincial Park 47.835030N, 59.337496W; 2                                  | heath   | moss      | 05-Jun-10     | Joe Brazil    | 10.06.05.av07        | DAOM744410                           |
| MH473373g                        | CANADA, NL, Searston Provincial Park 47.835030N, 59.337496W; 2                                  | heath   | moss      | 05-Jun-10     | Andrus Voitk  | 10.06.05.av05        | DAOM744409                           |
| MH473377i                        | CANADA, NL, Gros Morne National Park, trail to Wigwam Lake 9.430075N, 57.744673W; 68         | fen     | *Sphagnum* | 01-Nov-05     | Andrus Voitk  | 05.11.01.av01        | DAOM744405                           |
| MN992480 h                       | CANADA, QC                                                                                      |          |           | 09-Sep-15     | Renee Lebeuf  | ANT255-HRL2125       |                                       |
| MN992479 h                       | CANADA, QC                                                                                      |          |           | 09-Sep-15     | Renee Lebeuf  | ANT256-HRL2124       |                                       |
| UDB032201 c                      | CANADA, NL, Labrador, L’Anse l’Amour sand dunes 51.476°N, 56.874°W; 4 m asl                   | sand dune | moss      | 16-Aug-08     | Esteri Ohenoja| LS-156 (ad3)         | TUF117473                             |
| UDB032202 c                      | CANADA, NL, Sandy Cove (GNP) 21U, NAD83, 5523750, N5689462                                     | limestone | barrens   | 5-Oct-16      | Michael Burzynski| 16.10.05.av06     | TUF117475                             |
| UDB032728 c                      | CANADA, NL, Labrador, outside Forteau 51.476°N, 56.874°W; 4 m asl                               | peat     | heath     | 5-Sep-05      | Tony Wright    | GM5-443               | TUF117474                             |
| UDB011424 c                      | ESTONIA                                                                                         | old firepit site | heath | 31-Oct-07 | Vello Liiv | TUF106200           |                                       |
| MH473369g                        | CANADA, NL, Ferolle Point 51.020619N, 57.094016W; 6                                           | heath   | *Sphagnum & moss* | 29-Jun-05 | Andrus Voitk  | 05.06.29.av01        | DAOM744403                           |
| MH473370 i                       | CANADA, NL, Great Brehat, Great Brehat moor 51.426534N, 55.498613W; 14                         | heath   | *Sphagnum & moss* | 09-Jun-10 | Andrus Voitk  | 10.07.09.av02        | DAOM744404                           |
| MH473372 i                       | CANADA, NL, Gros Morne National Park, Western Brook Pond trail 49.786176N, 57.862653W; 24  | bog     | *Sphagnum* | 09-Jun-07    | Andrus Voitk  | 07.09.06.av08        | DAOM744406                           |
| MH473376 i                       | CANADA, QC, Saint-Augustin, Saint-Augustin archipelago 51.175867N, 58.479824W; 2            | bog     | *Sphagnum* | 24-Jul-07    | Andrus Voitk  | 07.07.24.av01        | DAOM744412                           |

\(^a\) *Omphalina pyxidata* complex, unidentified species; most recorded as “*Omphalina cf. pyxidata*”

\(^b\) Arranged in the order they appear in Fig. 1, followed by sequenced species not in Fig. 1

\(^c\) Sequence generated at Tartu University

\(^d\) Sequence generated at the Field Museum

\(^e\) Voucher collection lost in transit on return from sequencing

\(^f\) Sequence generated by Osmundson et al. (2013)

\(^g\) Sequence generated at Bridgewater College

\(^h\) Sequence generated by Landry & Bérubé, direct submission to GenBank, no associated publication
Table 3  Specimens of sphagnicolous arrhenias examined

| GenBank number top, UNITE below | Phylogenetic IDa | Country, state/province, town, locality above, coordinates (degree decimal); elevation (m asl) below | Habitat above, substrate below | Date | Collector above, collection number below | Herbarium number: main above, copy below |
|--------------------------------|-----------------|-------------------------------------------------------------------------------------------------|--------------------------------------|------|----------------------------------------|--------------------------------------|
| OM422825c                       | *Arrhenia bigelowii* | Canada, NL, Labrador, Battle Harbour, Great Caribou Island, Indian Cove 52.267245°N, 55.591108°W; 38 | Bog Sphagnum                      | 21-Aug-18 | Michael Burzynski TCMB-16 | DAOM984945 TUF117649 |
| UDB038318                       |                 |                                                                                                   |                                      |      |                                        |                                      |
| OM422827c                       | *Arrhenia bigelowii* | Canada, NL, Labrador, Battle Harbour, Great Caribou Island 52.273339°N, 55.591108°W; 38        | Bog Sphagnum                      | 20-Aug-18 | Michael Burzynski CEMB-01 | DAOM984945 TUF117649 |
| UDB038320                       |                 |                                                                                                   |                                      |      |                                        |                                      |
| OM422828c                       | *Arrhenia bigelowii* | Canada, NL, Labrador, Battle Harbour, Great Caribou Island, Indian Cove 52.267245°N, 55.591108°W; 42 | Bog Sphagnum                      | 21-Aug-18 | Andrus Voitk TCAV-11 | DAOM984947 TUF117651 |
| UDB038322                       |                 |                                                                                                   |                                      |      |                                        |                                      |
| OM422830c                       | *Arrhenia bigelowii* | Canada, NL, Labrador, Battle Harbour, Great Caribou Island, Indian Cove 52.267245°N, 55.591108°W; 42 | Bog Sphagnum                      | 21-Aug-18 | Maria Voitk TCMV-01 | DAOM984950 TUF117652 |
| UDB038323                       |                 |                                                                                                   |                                      |      |                                        |                                      |
| MH473353c                       | *Arrhenia bigelowii* | Canada, NL, near Great Brehat, Great Brehat moor 51.426534°N, 55.498613°W; 14 | Bog Sphagnum                      | 09-Jul-10 | Andrus Voitk 10.07.09.av04 | DAOM744389 |
| MH473349d                       |                 |                                                                                                   |                                      |      |                                        |                                      |
| MH473350d                       | *Arrhenia bigelowii* | Canada, NL, near Botwood, New Bay Pond 49.099799°N, 55.581375°W; 111 | Bog Sphagnum                      | 26-Jul-06 | Andrus Voitk 07.06.23.av01 | DAOM744395 |
| MH473351d                       | *Arrhenia bigelowii* | Canada, QC, Saint-Augustin, Saint-Augustin archipelago 51.175867°N, 58.479824°W; 2 | Bog Sphagnum                      | 23-Jul-06 | Andrus Voitk 07.06.23.av03 | DAOM744395 |
| MH473352d                       | *Arrhenia bigelowii* | Canada, QC, Saint-Augustin, Saint-Augustin archipelago 51.175867°N, 58.479824°W; 2 | Bog Sphagnum                      | 23-Jul-07 | Andrus Voitk 07.07.23.av09 | DAOM744394 |
| MH473348c,e                      | *Arrhenia bigelowii* | Canada, NL, Rocky Harbour, Rocky Harbour bog 49.577694°N, 57.898916°; 35 | Bog Sphagnum                      | 05-Jul-04 | Andrus Voitk 04.07.05.av03 | DAOM744391 |
| MH473347c                       |                 |                                                                                                   |                                      |      |                                        |                                      |
| MH473346c                       | *Arrhenia bigelowii* | Canada, NL, Labrador, near Red Bay Tracy's Hill 51.729722°N, 56.447783°; 138 | Bog Sphagnum                      | 15-Jun-05 | Andrus Voitk 05.06.15.av01 | n/a* |
| MH473345c                       |                 |                                                                                                   |                                      |      |                                        |                                      |
| MH198227c                       | *Arrhenia bigelowii* | Germany, Bayern, Garmisch-Partenkirchen, Saulgrub | Sphagnum                         | 19-Jun-66 | Anders Dahlberg 86018 | GB-0072229 |
| UDB034637                       |                 |                                                                                                   |                                      |      |                                        |                                      |
| MH198189c                       | *Arrhenia bigelowii* | Finland, Pohjois-Savo, Vehmersalmi, Rytökylä | Sphagnum                         | 26-Sep-93 | Ilkka Kyöväri 92-147 | H6057135 |
| UDB024397                       |                 |                                                                                                   |                                      |      |                                        |                                      |
| MH198188c                       | *Arrhenia bigelowii* | Finland, Pohjois-Häme, Virrat, Hauhuu | Sphagnum                         | 05-Aug-90 | Ilkka Kyöväri 90-133 | H6057146 |
| UDB024396                       |                 |                                                                                                   |                                      |      |                                        |                                      |
| MH198195c                       | *Arrhenia bigelowii* | Germany, Bayern, Gemisch-Partenkirchen, Saulgrub | Sphagnum                         | 13-Jun-96 | Christoph Johannes Hahn | M-0276634 |
| UDB024405                       |                 |                                                                                                   |                                      |      |                                        |                                      |
| MH198192c                       | *Arrhenia bigelowii* | Sweden, Södermanland, Värdinge, Sjuvadskogen, between St. and L. Alsjön | Sphagnum                         | 09-Aug-94 | Klas Jaederfeldt S-F77529 |                                      |
| UDB024401                       |                 |                                                                                                   |                                      |      |                                        |                                      |
| MH198190c                       | *Arrhenia bigelowii* | Sweden, Uppland Hållnäs par., Lake Fräkensjön (= 4 km N of Hållnäs) | Sphagnum                         | 06-Aug-83 | Nils Lundquist 14499 | S-F277532 |
| UDB024398                       |                 |                                                                                                   |                                      |      |                                        |                                      |
| MH198219c                       | *Arrhenia bigelowii* | Canada, NL, Gros Morne National Park, bog at foot of Gros Morne Mt. 49.577694°N, 57.898916°W; 35 | Bog Sphagnum                      | 12-Aug-08 | Andrus Voitk 08.08.12.av05 | DAOM744390 TUF117583 |
| UDB034625                       |                 |                                                                                                   |                                      |      |                                        |                                      |
| MH198220c                       | *Arrhenia bigelowii* | Canada, NL, Labrador, Battle Harbour, Great Caribou Island, Indian Cove 52.2668°N, 55.648°W; 17 | Bog Sphagnum                      | 19-Aug-08 | Andrus Voitk BH-018 (IC57) | TUF117584 |
| UDB034626                       |                 |                                                                                                   |                                      |      |                                        |                                      |
| MH198204c                       | *Arrhenia bigelowii* | Germany, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald | Sphagnum                         | 05-Jul-05 | Doris Laber KR-0003833 |                                      |
| GenBank number top, UNITE below | Phylogenetic ID<sup>0</sup> | Country, state/province, town, locality above, coordinates (degree decimal); elevation (m asl) below | Habitat above, substrate below | Date | Collector above, collection number below | Herbarium number: main above, copy below |
|-------------------------------|--------------------------|---------------------------------------------------------------------------------------------------|-------------------------------|------|------------------------------------------|---------------------------------------------|
| MH198205<sup>5</sup> UDB032053 | Arrhenia bigelowii       | Germany, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald                               | 18-Jul-84                      | Doris Laber KR-0004262                        |                                          |
| MH198207<sup>5</sup> UDB032056 | Arrhenia bigelowii       | GERMANY, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald                              | 19-Aug-06                     | Doris Laber KR-0004519                        |                                          |
| MH198206<sup>5</sup> UDB032054 | Arrhenia bigelowii       | Germany, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald                              | 08-Sep-03                      | Doris Laber KR-0004576                        |                                          |
| OM422833<sup>5</sup> UDB038353 | Clitocybe gerardiana var. fusca | USA, MICH, Luce co., Pike Lake Bog Sphagnum                                              | 11-Sep-53                     | A. H. Smith 42574                            | MICH10143 TUF117871                       |
| OM422824<sup>4</sup> UDB038317 | Arrhenia bigelowii       | Canada, NL, Labrador, Battle Harbour, Great Caribou Island 52.273339°N, 55.591108°W; 38 | 20-Aug-18                      | Michael Burzynski CEMB-02                    | DAOM984946 TUF117646                     |
| OM422832<sup>4</sup> UDB038325 | Arrhenia bigelowii       | Canada, NL, Labrador, Battle Harbour, Great Caribou Island, Indian Cove 52.267245°N, 55.629755°W; 42 | 21-Aug-18                      | Michael Burzynski TCMB-09                    | DAOM984948 TUF117657                     |
| MH473354<sup>4</sup>          | Arrhenia bigelowii       | Canada, NL, near Stephenville 48.542358N, 58.118079W; 24                                      | 08-Aug-07                     | Andrus Voitk 07.08.08.av02                    | DAOM744392 M-0276635                     |
| MH473355<sup>4</sup> UDB0802694 | Arrhenia bigelowii       | Canada, NL, Stephenville Crossing, 48.516017N, 58.433798W; 16                               | 17-Aug-10                     | Andrus Voitk 10.08.17.av01                    | DAOM744392 TUF117886                     |
| MH198199<sup>5</sup> UDB032042 | Arrhenia gerardiana      | Germany, Fürstenfeldbruck                                                               | 24-Jun-73                     | Andreas Bresinsky M-0276635                   |                                         |
| MH198191<sup>5</sup> UDB024399 | Arrhenia gerardiana      | Sweden, Dalarna, Orsa par., Tunturi, NE of Mt. Stora (22 km N of Skattungbyn)                | 10-Aug-93                     | Nils Lundquist 19520                          | S-F277528                                |
| MH473366<sup>4</sup>          | Arrhenia gerardiana      | Canada, NL, Gros Morne National Park, Western Brook Pond trail 49.786176N, 58.626535W; 24 | 15-Jun-06                     | Andrus Voitk 06.06.15.a-v04                   | DAOM744373                               |
| MH473357<sup>4</sup> MH473358<sup>4</sup> | Arrhenia gerardiana    | Canada, NL, Cheesman Park 47.632104N, 59.256736W; 3                                         | 15-Jul-04                     | Andrus Voitk 04.07.15.a-v01                   | DAOM744371                               |
| MH473359<sup>4</sup>          | Arrhenia gerardiana      | Canada, NL, Rocky Harbour, Rocky Harbour bog 49.577694N, 57.898916W; 35                  | 03-Jul-05                     | Andrus Voitk 05.07.03.av01                    | DAOM744376                               |
| MH473355<sup>4</sup>          | Arrhenia gerardiana      | Canada, NL, Rocky Harbour, Rocky Harbour bog 49.577694N, 57.898916W; 35                  | 03-Jul-05                     | Andrus Voitk 05.07.03.av02                    | DAOM744377                               |
| MH473367<sup>4</sup>          | Arrhenia gerardiana      | Canada, NL, Rocky Harbour, Rocky Harbour bog 49.577694N, 57.898916W; 35                  | 03-Jul-05                     | Andrus Voitk 05.07.03.av03                    | DAOM744375                               |
| MH473365<sup>4</sup>          | Arrhenia gerardiana      | Canada, NL, near Gillams, Gillams bog 49.011140N, 58.066273W; 103                      | 16-Jul-08                     | Andrus Voitk 08.07.16.av01                    | DAOM744372                               |
| MH473361<sup>4</sup>          | Arrhenia gerardiana      | Canada, QC, Saint-Augustin, Saint-Augustin archipelago 51.175867N, 58.479824W; 2       | 24-Jul-07                     | Andrus Voitk 07.07.24.av02                    | DAOM744387                               |
| MH47335<sup>4</sup>           | Arrhenia gerardiana      | Canada, QC, Saint-Augustin, Saint-Augustin archipelago 51.175867N, 58.479824W; 2       | 23-Jul-07                     | Andrus Voitk 07.07.23.av02                    | DAOM744386                               |
| MH473363<sup>4</sup>          | Arrhenia gerardiana      | Canada, QC, Saint-Augustin, Saint-Augustin archipelago 51.175867N, 58.479824W; 2       | 21-Jul-07                     | Andrus Voitk 07.07.21.av01                    | DAOM744384                               |
| MH473360<sup>4</sup>          | Arrhenia gerardiana      | Canada, NL, Rocky Harbour, Rocky Harbour bog 49.577694N, 57.898916W; 35                  | 15-Jun-06                     | Andrus Voitk 06.06.15.av02                    | DAOM744378                               |
| MH473362<sup>4</sup>          | Arrhenia gerardiana      | Canada, QC, Saint-Augustin, Saint-Augustin archipelago 51.175867N, 58.479824W; 2       | 23-Jul-07                     | Andrus Voitk 07.07.23.av01                    | DAOM744385                               |
| GenBank number top, UNITE below | Phylogenetic ID | Country, state/province, town, locality above, coordinates (degree decimal); elevation (m asl) below | Habitat above, substrate below | Date | Collector above, collection number below | Herbarium number: main above, copy below |
|---------------------------------|----------------|----------------------------------|----------------|------|----------------------------------------|---------------------------------|
| MH198183<sup>5</sup> UDB024327<sup>6</sup> | Arrhenia gerardiniana | USA, New York, Essex Co., North Elba, Mount Marcy | Bog | Undated | Charles Peck | NYDs4725.1 |
| MH198221<sup>1</sup> UDB034627 | Arrhenia gerardiniana | Canada, NL, Labrador, Battle Harbour, Great Caribou Island, Indian Cove 52.2668N, 55.648W; 17 | Bog | 19-Aug-08 | Maria Voitk BH-020 (IC54) | DAOM744382 TUF117585 |
| MH198222<sup>2</sup> UDB034628 | Arrhenia gerardiniana | Canada, NL, Labrador, Battle Harbour, Great Caribou Island, Indian Cove 52.2668N, 55.648W; 17 | Bog | 19-Aug-08 | Anne Marceau BH-022 (IC55) | TUF117586 |
| MH198223<sup>3</sup> UDB034629 | Arrhenia gerardiniana | Canada, NL, Labrador, Battle Harbour, Great Caribou Island, Indian Cove 52.2668N, 55.648W; 17 | Bog | 19-Aug-08 | Maria Voitk BH-021 (IC56) | TUF117587 |
| MH198224<sup>4</sup> UDB034631 | Arrhenia gerardiniana | Canada, NL, Rocky Harbour, Rocky Harbour bog 49.577694N, 57.898916W; 35 | Bog | 04-Jul-17 | Michael Burzynski | DAOM744379 TUF117590 |
| MH198225<sup>5</sup> UDB034632 | Arrhenia gerardiniana | Canada, NL, Rocky Harbour, Rocky Harbour bog 49.577694N, 57.898916W; 35 | Bog | 05-Jul-17 | Michael Burzynski | DAOM744380 TUF117591 |
| MH198226<sup>6</sup> UDB034633 | Arrhenia gerardiniana | Canada, NL, Rocky Harbour, Rocky Harbour bog 49.577694N, 57.898916W; 35 | Bog | 05-Jul-17 | Michael Burzynski | DAOM744381 TUF117592 |
| OM422826<sup>7</sup> UDB038319 | Arrhenia gerardiniana | Canada, NL, Labrador, Battle Harbour, Great Caribou Island 52.273339°N, 55.591108°W; 38 | Bog | 20-Aug-18 | Andrus Voitk | DAOM984942 TUF117648 |
| OM422831<sup>8</sup> UDB038324 | Arrhenia gerardiniana | Canada, NL, Labrador, Battle Harbour, Great Caribou Island 52.267245°N, 55.629755°W; 42 | Bog | 21-Aug-18 | Michael Burzynski | DAOM984944 TUF117653 |
| MH473364<sup>4</sup> | Arrhenia gerardiniana | Canada, NL, Gros Mornie National Park, Western Brook Pond trail 49.786176N, 57.862653W; 25 | Bog | 31-Aug-08 | Andrus Voitk 08.08.31.av02 | DAOM744374 |
| MH198218<sup>5</sup> UDB034624 | Arrhenia gerardiniana | Canada, Labrador, W of Konrad Brook Pond 56.139413N, 62.730548W; 50 | Bog | 28-Jul-08 | Esteri Ohenoja KL-014 (K42) | DAOM744383 TUF117581 |
| OM422828<sup>9</sup> UDB038321 | Arrhenia gerardiniana | Canada, NL, Labrador, Battle Harbour, Great Caribou Island 52.273339°N, 55.591108°W; 38 | Bog | 20-Aug-18 | Maria Voitk CEMV-02 | DAOM748494 TUF117650 |
| OM422836<sup>10</sup> UDB0802695 | Arrhenia gerardiniana | Canada, NL, near Stephenville | Bog | 13-Jul-10 | Andrus Voitk | TUF117887 |
| n/a<sup>11</sup> | Agaricus gerardinus | USA, New York | Bog | Undated | Charles Peck | NYf4339.1–4 |
| MH198198<sup>12</sup> UDB32176 | Arrhenia philonotis | Canada, NL, Labrador, L’Anse Amour 51.470074N, 56.870960W; 2 | Heath | 16-Aug-08 | Esteri Ohenoja LS-008 (AD-14) Pirkko Askola Tauno Toivonen 1413 | TUF117360 |
| MH198187<sup>13</sup> UDB024395 | Arrhenia philonotis | Finland, Uusimaa, Nurmijärvi, Kaikkala | Moss | 08-Jul-84 | | H6057134 |
| MH198203<sup>13</sup> UDB032501 | Arrhenia philonotis | Germany, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald | Bog | 29-Jul-84 | Doris Laber | KR-0003880 |
| MH198202<sup>13</sup> UDB032050 | Arrhenia philonotis | Germany, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald | Bog | 18-Aug-90 | Doris Laber | KR-0004132 |
| MH198194<sup>13</sup> UDB024404 | Arrhenia philonotis | Germany, Oberbayern, Moor am Eßsee | Bog | 28-Jun-58 | J. Poelt | M-0276633 |
| MH491520<sup>13</sup> | Arrhenia philonotis | Canada, NL, Labrador, Konrad Brook 56.278381N, 62.933697W; 517 | Bog | 30-Jul-08 | Michael Burzynski | DAOM744400 KL-013 (T13) |
| MH491521<sup>13</sup> | Arrhenia philonotis | Canada, NL, Labrador, L’Anse Amour 51.470074N, 56.870960W; 2 | Bog | 15-Aug-08 | Maria Voitk | n/a LS-010 (LAT4) |
| GenBank number top, UNITE below | Phylogenetic ID\(^a\) | Country, state/province, town, locality above, coordinates (degree decimal); elevation (m asl) below | Habitat above, substrate below | Date | Collector above, collection number below | Herbarium number: main above, copy below |
|-------------------------------|-------------------------|------------------------------------------------------------------------------------------------|-------------------|------|------------------------------------------|---------------------------------|
| MH198197<sup>c</sup> UDB032175 | *Arrhenia philonotis* | Canada, NL, Labrador, Konrad Brook 56.278381N, 62.933697W; 517 | Bog *Sphagnum* and moss | 30-Aug-08 | Andrus Voitk KL-015 (T3) | DAOM744401 TUF117359 |
| U66449<sup>b</sup> | *Arrhenia philonotis* | Greenland | | | | |
| MH473368<sup>d</sup> | *Arrhenia philonotis* | Norway, near Tromse, Kaldfjord 69.679009N, 18.737086E; 75 | Fen *Moss and Sphagnum* | 06-Jul-08 | Andrus Voitk 08.07.06.av01 | DAOM744402 |
| OM422834<sup>e</sup> UDB039743 | *Agaricus telmatiaeus* (HOLOTYPE) | UK, England, Yorkshire County, Scarborough | | | | |
| MH198211<sup>f</sup> UDB032770 | *Arrhenia telmatiaea* | Germany, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald | Bog *Sphagnum* | 05-Oct-86 | Doris Laber KR-0004131 | |
| MH198201<sup>g</sup> UDB032049 | *Arrhenia telmatiaea* | Germany, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald | Bog *Sphagnum* | 03-Oct-04 | Doris Laber KR-0004167 | |
| MH198200<sup>h</sup> UDB032048 | *Arrhenia telmatiaea* | Germany, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald | Bog *Sphagnum* | 10-Oct-07 | Doris Laber KR-0004666 | |
| MH198196<sup>i</sup> UDB032174 | *Arrhenia telmatiaea* | Canada, NL, L’Anse aux Meadows 51.594895N, 55.533285W; 6 | Bog *Sphagnum* | 18-Sep-12 | Andrus Voitk GNP-064 | TUF117357 |
| MH198210<sup>j</sup> UDB032723 | *Arrhenia telmatiaea* | Canada, NL, Labrador, Trans Labrador Highway 52.899521N, 57.161205W; 374 | Bog *Sphagnum* | 14-Sep-16 | Maria Voitk 16.09.14.av01 | DAOM744398 TUF117458 |
| MH198214<sup>k</sup> UDB034619 | *Arrhenia telmatiaea* | Estonia, Tartu Co., Puhja Comm. | | | | |
| MH198228<sup>l</sup> UDB034638 | *Arrhenia telmatiaea* | Sweden, Västra Götaland Co., Essunga Comm., Bäreberg | | | | |
| MH198184<sup>m</sup> UDB024392 | *Arrhenia telmatiaea* | Finland, Varsinais-Suomi, Vihti, Iso Sammakko | | | | |
| MH198186<sup>n</sup> UDB024394 | *Arrhenia telmatiaea* | Finland, Etelä-Häme, Lempäälä, Hietaniemi | | | | |
| MH198185<sup>o</sup> UDB024393 | *Arrhenia telmatiaea* | Finland, Uusimaa, Kirkkonummi, Väransby | | | | |
| MH198182<sup>p</sup> UDB024581 | *Omphalina fusconigra* (HOLOTYPE) | UK, Scotland, South Perthshire, Blair Drummond | | | | |
| MH198193<sup>q</sup> UDB024402 | *Arrhenia telmatiaea* | Germany, Bayern, Garmisch-Partenkirchen, Fügsee | | | | |
| MH198213<sup>r</sup> UDB034618 | *Arrhenia telmatiaea* | Estonia, Ida-Viru Co., Sirts swamp | | | | |
| MH198216<sup>s</sup> UDB034621 | *Arrhenia telmatiaea* | Estonia, Pärnu Co., Nigula bog | | | | |
| MH198217<sup>t</sup> UDB034622 | *Arrhenia telmatiaea* | Estonia, Tartu Co., Ahunapulu | | | | |
| MH198215<sup>u</sup> UDB034620 | *Arrhenia telmatiaea* | Estonia, Ida-Viru Co., Sirts swamp | | | | |
| MH198212<sup>v</sup> UDB034617 | *Arrhenia telmatiaea* | Canada, NL, Labrador, Trans Labrador Highway near Red Bay 51.749723N, 56.420208W; 27 | Bog *Sphagnum* | 07-Sep-05 | Tony Wright 05.09.07.av01 | DAOM744399 TUF117580 |
| U66453<sup>w</sup> | *Arrhenia telmatiaea* | Greenland, Disco | | | | |
| MH198229<sup>x</sup> UDB034639 | *Arrhenia telmatiaea* | Sweden, Västra Götaland Co., Trollhättan Comm., Björndalen | | | | |

\(^a\) Phylogenetic ID: UDB03 | \(^b\) GenBank number: U66449 | \(^c\) UNITE number: MH198197c | \(^d\) UNITE number: MH473368d | \(^e\) UNITE number: OM422834e | \(^f\) UNITE number: UDB039743f | \(^g\) UNITE number: MH198211gf | \(^h\) UNITE number: UDB032049h | \(^i\) UNITE number: MH198210if | \(^j\) UNITE number: UDB032723ij | \(^k\) UNITE number: MH198214ik | \(^l\) UNITE number: UDB0346191l | \(^m\) UNITE number: MH198184m | \(^n\) UNITE number: UDB024392n | \(^o\) UNITE number: MH198186on | \(^p\) UNITE number: MH198182pp | \(^q\) UNITE number: UDB024581qq | \(^r\) UNITE number: MH198193rq | \(^s\) UNITE number: UDB024402sr | \(^t\) UNITE number: MH198213ut | \(^u\) UNITE number: UDB034618u | \(^v\) UNITE number: MH198216tv | \(^w\) UNITE number: UDB034621uw | \(^x\) UNITE number: MH198229wx | \(^y\) UNITE number: UDB034639yx |
the brown *Arr. gerardiana*, but lighter specimens are indistinguishable from the latter (Fig. 4a, e). Occasionally the scales disappear from some very mature (caps over 20 mm in diameter) specimens of *Arr. gerardiana* (Figs. 3d and 4f), possibly through loss of the outer pileipellis layer, making such specimens difficult to distinguish from similar smooth-capped taxa, particularly the *Omphalina* sp. *Arrhenia philonotis* and *Arr. telmatiaea*, the two smooth-capped species (Fig. 5) in the more derived lineage, have mature cap diameters over 20 mm, at times reaching over 35. Fine adpressed hairs outlining similar radially arranged scale shapes with centrifugal points are spread sparsely about the cap of *Arr. philonotis*, occasionally rising to form scattered thin hairs, better observed with magnification (Fig. 3e). Rudimentary outlines of similar scales can be seen in the pileipellis of *Arr. telmatiaea* as well (Fig. 3f, g), which remain adpressed without tips rising up. The original descriptions of both *Agaricus telmatiaeus* and *Omphalina fusconigra* fit the dark smooth-capped species (Fig. 5c–e). Orton’s description of the cap texture was confirmed by our observations: the cap of 17 basidiomata can be observed on photos of eight collections confirmed by molecular studies to be conspecific with *O. fusconigra*. All caps are smooth, but one rather old basidioma reveals scurfy-flocculose texture limited to the depth of the navel. In other words, this is not a scaly capped species, but just as Orton described, a smooth-capped species, which only on occasion (<6% of basidiomata in our experience) develops wrinkling irregularity in the depth of its navel. The *Omphalina* sp. (Fig. 5f, g) has the largest basidiomata, occasionally over 35-mm cap diameter, a smooth cap, and a colour that leans more toward reddish than greyish brown. When found in *Sphagnum*, it can add to the confusion of identifying these species.

**Micromorphology**

All species have clamp connections through all tissues, primarily 4-spored basidia, and lack cystidia. Basidiospores of *Arr. telmatiaea* are the smallest, averaging $7.3 \times 4.7 \mu m$, separating it from *Arr. philonotis*, averaging $8.7 \times 5.6 \mu m$, most of the time. Basidiospores of the scaly capped species are longer and narrower than the spores of the smooth-capped species, but do not separate well from each other (Fig. 6).
Those of *Arr. gerardiana* are smaller than those of its sometimes darkening sister, but the majority cluster in the overlapping section, making measurement a helpful differentiator only at the extremes of their combined range.
The pileipellis of all four species consists of repent clamped hyaline cells with a modest to moderately copious amount of incrusted brownish pigment, some evident as small plates on the cell wall (Fig. 7a–d). Incrustation is most obvious in the scaly capped species and least in the hyaline hyphae of Arr. telmatiaea, where incrustation is subtle and requires time to find. The scales of Arr. bigelowii and Arr. gerardiana resemble each other, fascicles of thick pileipellis hyphae turning to project upwards to form a visible acute tipped scale (Fig. 7e, f), with unpigmented clear rounded terminal cells.

**Ecology and distribution**

Three species were observed to be obligated sphagnophiles. Of these, the two scaly capped species, Arr. gerardiana and Arr. bigelowii, were sympatric, on occasion found in the same bog at the same time. The dark smooth-capped Arr. telmatiaea was also an obligate sphagnophile. The smooth-capped Arr. philonotis was a facultative sphagnophile, growing in bogs, heaths, moors, and other exposed places, among Sphagnum, but at least equally often with other mosses. The Omphalina sp. was collected from bogs with Sphagnum (Fig. 5g) or heaths and moors with other mosses, but was far more common in grasslands with low moss (Fig. 5f). All four species of Arrhenia were distributed throughout both Europe and North America (including Greenland). In NL smooth-capped arrhenias were more northerly, found in Labrador, the Great Northern Peninsula, and along the northern east coast, bathed by the Labrador Current. The scaly capped species extended throughout the province. The Omphalina sp. shared the same distribution with the scaly capped species in NL, and matched GenBank sequence JF908501 and UNITE sequence UDB011424, confirming its presence in Europe.

**Taxonomy**

**Arrhenia bigelowii** Voitk, Lickey & I. Saar, sp. nov. Fig. 3a; 4a–d; 7a, e, f.

*Typefication:* CANADA, NL, Rocky Harbour bog, 49.577694°N, 57.898916°W, 35 m asl, bog in Sphagnum, 5 Jul 2005, leg. Andrus Voitk 04.07.05.av03. (DAOM744391, holotype)

= *Clitocybe gerardiana* var. *fusca* H.E. Bigelow, Mycologia 50(1):401. 1958. USA, MI, Luce Co., Pike Lake, bog in Sphagnum, 11 Sep 1953, leg. Alexander H. Smith, 42574 (MICH 10143, varietal holotype). Ibid; a solitary partial pileus donated from the holotype collection MICH 10143 to TUF, and accessioned as an isotype (TUF117871! varietal isotype, GenBank MH473348).

*Etymology:* Bigelowii honours the American mycologist Howard Elson Bigelow, the first to publish this entity as a separate taxon.

**Diagnosis.** Basidioma 8–33 mm tall, in Sphagnum; cap usually under 20-mm diameter, brown, umbilicate, radially striate, scaly; gills decurrent, light brown; stem light brown; obligate sphagnophilic denizen of temperate to subarctic raised bogs. Pinnate scales distinguish it from smooth-capped sphagnophilic arrhenias; in addition to being somewhat darker most of the time, it can be separated from the other scaly capped sphagnicolous species, Arr. gerardiana, by an occasional darkening reaction, tendency for more inverted bowl shaped pilei, longer spores, and an ITS sequence difference of 37 base pairs.

**Capsule varietal isotype description.** Studied material was approximately one-half of a dried pileus with gills attached, approx. 1.5 cm in diam. Cap striate, umbilicate. Microscopic examination of a squash section of gill revealed elongate elliptical spores 6.1–11.4 × 3.2–4.9 μm (ave. 8.4 × 4.0, Q 1.7–2.5, ave. 2.1, n = 22 spores). No cystidia, but clamp connections readily evident. Four-spored club-shaped basidia, approx. size 34 × 7 μm. Cap structure not examined.

**Macromorphology** (Fig. 3a; 4a–d). Basidioma: Brown, stipitate, about 8–33 mm tall, in Sphagnum. Uncommonly becomes dusky, with various degrees of black and grey adding to or covering the brown colouration. Stimulus for this change not known. Pileus: 4–24-mm diameter, usually deeply umbilicate and often shaped like an inverted bowl, edges becoming more plane, then crenulate with age, transversely striate, covered with somewhat concentric radially arranged scales with darker brown, burr-like, uplifted, centripetally narrowing ends. Radially ribbed with darker narrow brown bands over lamellae and lamellulae, alternating with wider, tan intervening bands; the latter become sulcate with time. Cap margin darkens with time. Lamellae: moderately spaced, smooth edged, deeply decurrent, with usually three intervening, small lamellulae; developing a few low crossveins beyond maturity,forking very rare; light brown, developing darker edge. Stipe: 10–23 × 2–5 mm, cylindric, straight; becoming somewhat hollow; brown; minutely tomentose, glabrescent with age, sparse white tomentum at base. Context: whitish, odour unremarkable.

**Micromorphology:** Basidiospores (369 spores, 18 basidiomata, 18 collections, 3 observers) 6.1–17.0 × 3.0–6.1 μm, ave. 10.3 × 4.6 μm, elongate elliptical, Q = 1.6–3.3, ave. 2.3, content homogeneous, some variation in size and shape between individual basidiomata (Fig. 6). Basidia 29–39 × 6.2–8.8 μm, ave. 35 × 7.4 μm; mostly four-spored with occasional two-spored; clavate, hyaline. No pleuro-, cheilo-, or caulocystidia, but terminal hyphal cells protrude from stipe as small hairs. Pileipellis a cutis with thin-walled, clamped hyphae, 3.5–13.5 μm wide, hyaline to brownish, with moderately incrusted brown pigment, superficial layers forming small plates on the cell surface (Fig. 7a). Scale tips end with
this gives an opportunity to honour Bigelow, the first to recognize this species a new taxon.

**Arrhenia gerardiana** (Peck) Elborne, Funga Nordica: 913. 2008. FIG. 3b–d; 4 e,f; 7g, h

Basionym: *Agaricus* (*Clitocybe*) *gerardinus* Peck, Bull. Buffalo Soc. Nat. Sci. 1: 46. 1873.

Mycobank MB542211

Typification: USA: NEW YORK, Ulster Co, New Paltz, June, 1873 (approx.), in “sphagnous marshes”, leg. C.H. Peck. (NYSf 1339.1–4! Lectotype, here designated; MBT10005613). USA: NEW YORK, Rensselaer Co., Sand Lake, June, 1873 (approx.), in “sphagnous marshes”, leg. C.H. Peck. (paratype, NYSf 1340, not seen, possibly lost). USA: NEW YORK, Essex County, North Elba, Mt. Marcy, June, no year, leg. & det. C.H. Peck (as *Omphalia gerardiana*) M212-S29-4000(7794) (NYSd 4725.1!, epitype, here designated. Mycobank type number MBT10005614).

**Capsule lectotype description.** The lectotype collection NYSf 1339.1–4 consists of four dried dark brown basidiomata glued to sheets (.1 and .4 further secured with cloth tape), reasonably intact with pieces of stipe and pileus missing. Tallest approx. 5.5 cm high (stipe base to top of upturned cap edge), with widest cap diam. approx. 1.2 cm. Caps striate, umbilicate to funnel-shaped. Microscopic examination of a squash section of gill (3% KOH) from each of the four basidiomata revealed pip-shaped to elliptical spores 6.8–12.4 × 3.4–5.1 μm (ave. 9.2 × 4.2, ave. Q = 2.2, n = 100 spores). No cystidia. Clamp connections throughout all tissues. Four-spored (rarely two) club-shaped basidia, approx. size 24 × 7 μm. Cap structure not examined.

**Capsule epitype description.** The epitype collection NYSd 4725, consisted of ten relatively intact dried dark brown basidiomata, most taped or glued to sheets, with parts missing, and additional pieces with most of the basidiomata missing. Tallest approx. 5.5 cm high (stipe base to top of upturned cap edge), with widest cap diam. approx. 1.2 cm. Caps striate, umbilicate to funnel-shaped. The epitype was selected and designated NYSd 4725.1. Microscopic examination of a squash section of gill revealed pip-shaped to elliptical spores 7.9–11.5 × 3.3–4.2 μm (ave. 9.8 × 3.8, ave. Q = 2.6, n = 20 spores). No cystidia. Clamp connections throughout all tissues. Four-spored club-shaped basidia, approx. size 24 × 7 μm. Cap structure not examined.

**Macromorphology (Fig. 3b–d; Fig. 4e, f): Basidioma:** Brown, stipitate, about 10–35 mm tall, in Sphagnum. Pileus: 5–25 mm diameter, usually deeply umbilicate, edges curved down somewhat at the margin, but rarely assuming an inverted bowl shape, becoming plane, then crenulate with age, transluently striate, covered with somewhat concentric radially arranged scales with darker brown, buff-like, uplifted, narrow distal ends. These scales seem to recede with age, and occasional very mature specimens with large caps may have
a The dramatically scaly cap of Arr. bigelowii (08.08.12.av05), unlikely to be described by diminutives, “sparsely wooly” or “minutely squamulose”.

b Peck’s aquarelle of his Ag. gerardiana with evident scales (photo courtesy NYS).

c The equally obvious scaly cap of Arr. gerardiana (05.07.03.av02).

d The smooth cap of a very mature desquamated Arr. gerardiana (17.07.05.av05), making identification difficult.

e Cap of Arr. philonotis (KL-015) showing subtle “scale pattern” embedded in the pileipellis, occasionally elevated to create a scattering of very fine hairs.

f A brownish and lighter cap of Arr. telmatiaea (GNP-064). A pattern resembling the radial scales of Arr. bigelowii or Arr. gerardiana can be seen, but these remain entirely adpressed in the pileipellis, with no attempts of the tips to rise.

g Cap of a very dark Arr. telmatiaea (05.09.08.av02). The adpressed “scale pattern” in the pileipellis is present, although not as evident.
Fig. 4 Scaly capped sphagamicous arrhenias of NL in situ. Bars = 10 mm. 

a Arrhenia bigelowii (07.06.26.av01). 

b The darkening reaction, occasionally seen with Arr. bigelowii. Collection 04.07.05.av03, the type specimen and model for the FNL logo. 

c Arr. bigelowii collection 05.06.15.av01: in situ appearance at the time of collection. 

d Arr. bigelowii appearance when taken from collecting basket, ca. 3 h later—the most dramatic darkening reaction of Arr. bigelowii we have observed. 

e Arrhenia gerardiana (06.06.15.av04)—macroscopically indistinguishable from Arr. bigelowii. 

f (insert; photo: Michael Burzynski) A large overmature Arr. gerardiana specimen (17.07.04.av02) with scales no longer evident (see also Fig. 3d)
no distinctive scales (Figs. 3d; 4f). Narrow brown radial bands over lamellae and lamellulae, alternating with wider, tan intervening bands; the latter become minimally sulcate with time. Cap margin darkens with time. Lamellae: moderately spaced, smooth edged, deeply decurrent, usually with three intervening, small lamellulae; developing a few low crossveins beyond maturity, forking very rare; light brown, developing darker edge. Stipe: 10–25 × 2–5 mm, cylindric, straight; becoming somewhat hollow; minutely tomentose; may disappear with age, brown with sparse white tomentum at base. Context: whitish, odour unremarkable.

Micromorphology: Basidiospores (443 spores, 20 basiomata, 17 collections, 3 observers) 6.2–12.9 × 2.8–5.6 μm, ave. 8.9 × 4.2 μm, pip-shaped to elliptical, Q = 1.3–3.2, ave. 2.2, content homogeneous, some variation in size and shape between individual basiomata (Fig. 6). Basidia 28 (21–35) × 6.8 (5.6–9.0) μm; mostly four-spored with occasional two-spored; clavate, hyaline. No pleuro-, cheilo-, or caulocystidia, but terminal hyphal cells protrude from stipe as small hairs. Pileipellis a cutis with thin-walled, clamped hyphae, 2.5–9.5 μm wide, hyaline to brownish, with moderately incrusted brown pigment, superficial layers forming small plates on the cell surface (Fig. 7b). Scale tips end with gently swollen rounded unipointed clear cells (Fig. 7g, h). Clamp connections in all tissues.

Habitat: Open raised Sphagnum bogs in groups of 1–6 separate basidiomata, attached to living Sphagnum with white mycelial tomentum, associated with various bog plants such as Vaccinium oxycoccos, V. macrocarpon, Rubus chamaemorus, Empetrum nigrum, Andromeda polifolia, and various bog orchids, reeds, and grasses, June–September, most plentiful in July. May be found in the same bog at the same time as Arr. bigelowii.

Distribution: Europe and North America; suspect Holarctic distribution. In NL, throughout the province.

Additional specimens examined: See Table 3.

Comments: Its cap, scaly throughout, sets it apart from the latter as epitype for Arrhenia gerardiana, thus defining the clade in which it resides as that species.

Arrhenia philonotis (Lasch) Redhead, Lutzoni, Moncalvo & Vilgalys, Mycotaxon 83: 48. 2002. Fig. 3e; 5a, b; 7e

Basionym: Agaricus philonotis Lasch, Linnaea 3:394. 1828.

Typification: Holotype probably lost. GERMANY, Baden-Württemberg, Schwarzwald, Ks. Breisgau-Hochschwarzwald, Hinterzarten, Hinterzartener Moor, MTB/Q 8014/4. Sphagnum, 29 Jul 1984, leg. D. Laber, (Neotype, here designated: KR-0003880! Mycobank type number MBT10005615).

Capsule neotype description. The neotype collection KR-0003880 is fragmented with no completely intact basiomata. Larger pieces are parts of at least 4–5 pilei and twice that number of stems, suggesting that the original collection may have consisted of around 8–10 basiomata. Although fragmented, there is a generous amount of material, which otherwise seems to be in good shape. Small strands of moss are seen, including at least one stem attached to what seems to be Sphagnum. By extrapolation, the tallest dried basiomata is approx. 5 cm high (stipe base to top of upper cap edge), with widest cap diam. approx. 2.5 cm. Caps smooth, umbilicate. Microscopic examination of a squash section of gill revealed pip-shaped to elliptical spores 7.7–10.4 × 5.2–7.6 μm (ave. 8.9 × 5.8, ave. Q = 1.5, n = 20 spores). No cystidia. Clamp connections throughout all tissues. Four-spored club-shaped basidia, approx. size 24 × 7 μm. Cap structure not examined.

Macromorphology (Fig. 3e; 5a, b); Basidioma: Brown, stipe-like, about 10–38 mm tall, in heaths, bogs and moors with Sphagnum or other moss. Pileus: 5–30-mm diameter, umbilicate, edges curved down becoming plane and crenulate with age, translucently striate, smooth, often covered with thin, fibrillose, adpressed, flat scales, whose tips may become slightly uplifted as scattered thin hairs, denser in the umbilicus. Narrow brown radial bands over lamellae and lamellulae, alternating with wider, tan intervening bands; the latter may become sulcate with time, giving the cap a radially ribbed appearance. Cap margin darkens with time. Lamellae: moderately spaced, smooth edged, deeply decurrent, with 3–5 intervening, small lamellulae; may develop a few low crossveins beyond maturity, forking very rare; light brown, developing darker edge. Stipe: 10–25 × 2–5 mm, cylindric, straight; becoming somewhat hollow; minutely tomentose, glabrescent, brown with sparse white tomentum at base. Context: whitish, odour unremarkable.

Micromorphology: Basidiospores (102 spores, 5 basiomata, 5 collections, 2 observers) 6.6–10.9 × 4.2–7.7 μm, ave. 8.7 × 5.6 μm, pip-shaped to elliptical with Q = 1.2–2.1, ave. 1.6, content homogeneous, some variation in size and shape between individual basiomata (Fig. 6).
Fig. 5 Smooth-capped sphagnicolous omphalinoids of NL. Bars = 10 mm. a Arrhenia philonotis (KL-015), “normal” light colouring. b Arrhenia philonotis (LS-008), dark colouring. c Arrhenia telmatiaea (05.09.08.av02). The near-black dark brown colour readily distinguishes this species from the others most of the time. d Arrhenia telmatiaea (GNP-064). Lighter brown. e Arrhenia telmatiaea (16.09.14.av01) medium dark caps. Colours of caps as on photos d and e might be confused with other species. f Omphalina species (16.10.18.av01) from unfertilized and mossy grassland, revealing full spectrum of fruiting body appearance. This species and Arr. philonotis are both larger (mature cap diameter > 25 mm), smooth-capped, and brown. The reddish tones of Omphalina and the greyish tones of Arrhenia are not always as obvious as on these photos. g Omphalina species (07.07.24.av01) growing in Sphagnum.
Fig. 6 Basidiospores of studied species. a Average spore sizes of sequence-identified sphagnicolous omphalinoid collections, length in μm on x-axis, width on y-axis. H, holotype; Hv, varietal holotype; Ht, holotype of Ag. telmatiaeus; N, neotype; L, lectotype (4 basiomata if Arr. gerardiana, not sequenced); E, epitype.

b–f Basidiospores of the studied species. Upper white line marks 10 μm. 

b Arr. bigelowii, c Arr. gerardiana, d Arr. philonotis, e Arr. telmatiae, f Omphalina species
Fig. 7 Cap micromorphology. Scale bars 10 μm. 

a Incrusted pigment *Arr. bigelowii* (08.08.12.av05). 
b Incrusted pigment *Arr. gerardiana* (17.07.05.av05). 
c Incrusted pigment *Arr. philonoitis* (KL-015). 
d Incrusted pigment *Arr. telmatiaea* (05.09.08.av02), the same specimen as Fig. 3e, from the collection on Fig. 5c. 
e Scales of *Arr. bigelowii* (10.08.17.av01). 
f Swollen, hyaline terminal hyphae of scale tip of *Arr. bigelowii* (same scale as e). 
g Swollen, hyaline terminal hyphae of scale tip of *Arr. gerardiana* (same scale as h). 
h Scales of *Arr. gerardiana* (10.07.13.av06)
Basidia 29.6 (23.3–35.2) × 7.8 (6.1–10.2) μm; mostly four-spored with occasional two-spored; clavate, hyaline. No pleuro-, cheilo-, or caulocystidia, but terminal hyphal cells protrude from stipe as small hairs. Pileipellis a cutis with thin-walled, clamped hyphae, 2.0–11.0 μm wide, hyaline to brownish, with moderately incrusted brown pigment, superficial layers forming small plates on the cell surface (Fig. 7c). Clamp connections in all tissues.

**Habitat:** Barren moors, heaths, fens, raised Sphagnum bogs in groups of 1–6 separate basidiomata, either with Sphagnum or other moss. Associated with various heath plants such as Vaccinium oxyccocos, V. macrocarpon, Rubus chamaemorus, Empetrnum nigrum, Andromeda polifolia, reeds and grasses, June–September, most plentiful in August.

**Distribution:** Known from North America and Europe; Holarctic distribution suspected; not as southerly as the scaly capped species, in NL so far known only from Labrador.

**Additional specimens examined:** See Table 3.

**Comments:** Basiomata resemble those of the scaly capped species, but are readily distinguished by their obviously smooth caps of somewhat greater diameter, and light colour tending more to greyish brown. Distinguished from Arr. telmatiae by its lighter hue and from the Omphalina species by its greyish rather than reddish brown hues and broader spores.

**Arrhenia telmatiae** (Berk. & Broome) Voitk & I. Saar, comb. nov. Fig. 3f,g; 5c, d, e; 7d

MycoBank MB842881

Basionym: *Agaricus telmatiae* Berk. & Cooke. Illustrations of British fungi (Hymenomycetes). Williams and Norgate, London. 2: pl 240. UK, England, Yorkshire Co., Scarboro, 2 Nov 1882, leg. G. Massee (NY12555, holotype!)

≡ *Omphalina fusconigra* P.D. Orton, Transactions of the British Mycological Society 43(2): 335. 1960. MycoBank MB518174. UK, Scotland, South Perthshire, Blair Drummond, 28 Sep 1957, leg. J. Grainger (K(M) 98588! holotype!).

≡ *Arrhenia fusconigra* (P.D. Orton) P.A. Moreau & Courtec., Documents Mycologiques 34 (135–136): 48 (2008).

Capsule holotype description. The holotype collection NY12555, consisted of eight relatively intact dried dark brown basidiomata with adherent Sphagnum, most taped or glued to sheets, with parts missing. Tallest approx. 4.8 cm high (stipe base to top of cap), with widest cap diam. approx. 3.8 cm. Caps striate, umbilicate. Microscopic examination of a squash section of gill revealed pip-shaped to elliptical spores 6.0–8.1 × 3.9–5.8 μm (ave. 7.2 × 4.7, Q = 1.3–1.8, ave. 1.5, n = 30 spores). No cystidia. Clamp connections throughout all tissues. Four-spored club-shaped basidia, approx. size 26 × 7 μm. Cap structure not examined.

**Macromorphology** (Fig. 3f, g; 5c,d,e): Basidioma dark brown, usually almost blackish, stipitate, about 10–40 mm tall, in Sphagnum. Pileus: 6–32 mm diameter, usually deeply umbilicate, edges curved down in a pronounced arc, becoming plane and then funnel-shaped with age, translucently striate, smooth, with occasional fine, fol-ecules in the umbilicus. Usually dark brown verging on black, but occasionally may remain mostly brown; dark, narrow, radial bands over lamellae and lamellulae, alternating with somewhat lighter deep brown bands; hygrophanous. Cap margin darkens with time. Lamellae: closely spaced, smooth edged, deeply decurrent, with usually 5–7 intervening lamellulae; forking very rare; medium to dark brown, edge darker. Stipe: 10–28 × 2–6 mm, cylindric, straight; becoming somewhat hollow; minutely tomentose, glabrescent, concolorous with pileus with sparse white tomentum at base. Context: lighter brown, odour unremarkable.

**Micromorphology:** Basidiospores (241 spores, 12 basiomata, 12 collections) 5.3–11.3 × 3.3–6.6 μm, ave. 7.3 × 4.7 μm, pip-shaped to elliptical, Q = 1.2–2.2, ave. 1.6, content homogeneous, some variation in size and shape between individual basiomata (Fig. 6). Basidia 27.6 (21.8–31.6) × 7.1 (5.5–8.6) μm, average 28.0 × 6.6; mostly four-spored with occasional two-spored; clavate, hyaline. No pleuro-, cheilo-, or caulocystidia, but terminal hyphal cells protrude from stipe as small hairs. Pileipellis a cutis with thin-walled, clamped hyphae, 3.5–9.0 μm wide, hyaline to brownish, with sparsely to moderately incrusted brown pigment, superficial layers at times forming small plates on the cell surface (Fig. 7d). Clamp connections in all tissues.

**Habitat:** Open raised Sphagnum bogs in groups of 1–6 separate basiomata, attached to living Sphagnum with white mycelial tomentum, associated with various bog plants such as Vaccinium oxyccocos, V. macrocarpon, Rubus chamaemorus, Empetrnum nigrum, Andromeda polifolia, reeds and grasses, July–September, most plentiful in August. May be found in the same bog at the same time as other northern species.

**Distribution:** Known from North America and Europe; suspected Holarctic distribution; in NL not as southern as the scaly capped species, so far known only from Labrador.

**Specimens examined:** See Table 3.

**Comments:** Its obviously and relatively even dark colour distinguishes it from the other smooth-capped sphagnicolous species, Arr. filonotis, but on occasion may be more dark brown than near-black, requiring microscopic examination to confirm identification. *Omphalister borealis* (M. Lange & Skife) Lamoure— not recorded in NL to date—is macroscopically very similar, also occurring in northern or alpine raised Sphagnum.
bogs, but can be distinguished by its globose, spinulose spores (Vašutová et al. 2013).

### Dichotomous key to the species of treated sphaginicolous omphalinoids in NL

1a. Granular green lichen thalli at base of stem and lack of clamp connections ........................................ Lichenomphalia

1b. No thalli at base of stem, and clamp connections ............. 2

2a. Cap scaly with raised, pointed, often darkened scale tips ... 3

2b. Cap smooth (may be minutely wrinkled, irregular or woolly, or may have adpressed scales, but not with raised scale tips) ................................................................. 4

3a. May undergo significant darkening reaction, spores 6.1–17.0 × 3.0–6.1 μm, ave. 10.3 × 4.6 μm .... Arrhenia bigelowii

3b. No darkening reaction, spores 6.2–12.9 × 2.8–5.6 μm, ave. 8.9 × 4.2 μm .............................. Arrhenia gerardiana

4a. Medium (=reddish) brown, mature cap around 30 mm diameter, spores <5 μm wide, distribution throughout NL .................................. Omphalina sp.

4b. Not as above; more greyish brown colours ............... 5

5a. Dark brown, nearly black, northerly distribution, obligate sphagnophile, spores 5.3–11.3 × 3.3–6.6, ave. 7.3 × 4.7 ............................... Arrhenia telmatiaea

5b. Medium to light grey-brown, northerly distribution, facultative sphagnophile, spores 6.6–10.9 × 4.2–7.7, ave. 8.7 × 5.6 ........... Arrhenia philonotis

### Discussion

Two characters have been particularly troublesome for nomenclatural consistency in the past. The first is lack of an early name for the common scaly capped sphaginicolous arrhenias, resulting in the application of incompatible epithets like tigrinus and affricatus to this group, or overinterpreting descriptions of cap vestiture in an effort to shoehorn the description to fit “scaly”, e.g. interpreting Lasch’s “leviter tomentosus” for Ag. philonotis as scaly instead of sparsely hairy, taking an occasional wrinkled umbilicus of O. fusconigra to mean a consistently scaly cap, or equating Berkeley’s description of minute cap surface irregularity of Ag. sphagincola with the rough scaliness of sphaginicolous arrhenias. The second confusing character is dark hue. Fries contributed to this by synonymizing his Ag. oniscus with a light species in his protologue (Fries 1818) and sanctioning work (Fries 1821), but later (Fries 1867) applying the name to a different and dark species, causing the name to be applied to dark arrhenias (Voitk 2022). Variability of the truly dark species, Arr. telmatiaea, from opaque near-black (Fig 3g; 5b) to translucently striate dark brown (Fig. 5c, d), lightening even to tan on drying, increases the opportunity to confuse it with darker specimens of Arr. philonotis (Fig. 5b), desquamated older Arr. gerardiana (Fig. 3d; 4f), or the unexpected Omphalina species. In addition, the ill-understood darkening reaction, sometimes extreme (Fig 4b, d), of Arr. bigelowii adds further confusion to these two taxa.

Spore size is genetically determined, and functioned as an indicator of genetic lineage before the DNA era. Our four clades separated into three groupings by spore size (Fig. 6, Fig. 8a): one for each of the two smooth-capped species and one larger grouping for the two scaly capped ones, whose constituent members proved difficult to separate from each other due to a large area of overlap in spore size (as well as similar macroscopic appearance). Favre (1948), treating Omphalia sphagincola (Berk.) P. Karst. as a scaly capped species, stressed the wide variability of size and shape of its spores (7.5–15 × 3–6 μm; average 11–4.3), the ranges indicating that he must have included both Arr. gerardii and Arr. bigelowii under the name. A decade later Bigelow (1958) described the species with bigger spores as a separate taxon, but this was not adopted, even by him, and it took molecular studies to confirm his observation.

To get an idea of the consistency of name use by the major pre-DNA workers cited in the “Introduction”, we plotted the spore size ranges for our four species (Fig. 8a), and then superimposed the spore measurements reported for each name by the same leading workers (Fig. 8). Full ranges, including extremes, were used for each, save for Lange and Lange (1982), who reported only the range of average values. The overall pattern was reasonably similar to ours: a cluster around each of the two smooth-capped species, and one covering both scaly capped ones (Fig. 8b), which suggests that the same four species were studied. Figure 8c–j shows spore sizes reported for each name used, distributing the eight names among half that number of species. The epithets most often applied to this group by the selected authors were oniscus and philonotis, both used in eight studies. Interestingly, spore measurements of seven of the eight species to which oniscus was applied (Fig. 8d), fit with those of Arr. telmatiaea; the measurements reported by Kuyper (1995) seem to fit better with Arr. philonotis while his measurements for the epithet philonotis seem to fit better with our telmatiaea. The relatively good fit of spore measurements to one epithet may tempt one to consider conserving oniscus over telmatiaea, until one notes that epithets other than oniscus have also been applied to species with spores matching those of Arr. telmatiaea: fusconigra (Bon 1997, Clément 1982; but not Bigelow 1985), icmadophila (Bigelow 1958; Redhead 1979), epicichysium (Lange and Lange 1982), and philonotis (Kuyper 1995; Lange and Lange 1982).

What consistent species concept may have been indicated by spore size loses most of its validity once other characters are considered. For example, our observations suggest that Arr. telmatiaea is an obligatory sphagnophile, fitting the illustration of the type by Massee depicting basidiomata intimately
attached to Sphagnum, and the several descriptions of Messrs Berkeley, Broome and Cooke, all stating that it occurs “in Sphagnum”. Of the eight studies applying oniscus to a species whose spore measurements fit those of Arr. telmatiaeae, only one (Gminder 2001) described it as an obligatory sphagnophile. Five (Favre 1948; Clémençon 1982; Bigelow 1985; Breitenbach and Kränzlin 1991; Elborne 2012) described it as a facultative sphagnophile, and two (Kuyper 1995; Bon 1997) stated that it grew with other mosses, but not with Sphagnum. Thus, some species other than Arr. philonotis must have also been considered part of the taxon to which oniscus had been applied. The most likely candidate is Arr. philonotis, which shares its darker colour, smooth cap, liking for moorland in cold climates, and a significant overlap of spore size, but not the obligatory relationship to Sphagnum. Thus, some species other than Arr. telmatiaeae must have also been considered part of the taxon to which oniscus had been applied. The most likely candidate is Arr. philonotis, which shares its darker colour, smooth cap, liking for moorland in cold climates, and a significant overlap of spore size, but not the obligatory relationship to Sphagnum.

Because it seemed to have the best potential for consistent application, we examined the epithet oniscus in detail. Similar inconsistency was observed with the three other species. Epithets with spore measurements fitting best with Arr. philonotis were philonotis (Favre 1948; Clémençon 1982; Bon 1997; Elborne 2008) and umbratilis (Lange and Lange 1982). Bon described the species as an obligatory sphagnophile, suggesting he had another species in mind. Epithets with spore measurements fitting best with the two scaly capped species were gerardiana (Bigelow 1958; Redhead 1979; Kuyper 1995; Elborne 2008), sphagnicola (Favre 1948; Clémençon 1982; Breitelbach & Kränzlin 1991; Bon 1997), and fusca (Bigelow 1958). In other words, past nomenclature has been inconsistent even in the hands of O. fusconigra) nests in this clade. Agaricus telmatiaeae has been left largely unused in the past, partly because of initial confusion around the name, and lack of a type specimen in Kew (Dennis 1948), all of which relegated it to a nomen dubium (Legon and Henrici 2005). Bigelow (1985) examined its type in NY, and recorded spore measurements that fit O. fusconigra. He stated these taxa should be compared, but because he was unable to confirm incrusted pigmentation, was uncertain about its correct placement. Examination of our own collections confirms that the species has incrusted pigment in its cap hyphae (Fig. 7d).
leading workers, by using multiple names for one species, by applying the same name to different species, and seemingly including more than one of the currently identified species under one name. Any nomenclatural reconciliation in this setting will result in instability to this small group of taxa. We identified Arr. philonotis as a facultative sphagnophile. Whether it interacts with Sphagnum at all or merely shares with it a like for similar habitats is a matter for investigation. Lücking (personal communication) states that philonotis is the commonest epithet applied to sphagnicolous arrhenias in European herbaria, which is disproportional to its prevalence among the four taxa, suggesting that unless A. philonotis is much commoner in Europe than NL, the name has been applied to more than one species. Our review suggests the latter. Molecular studies enabled us to name all other clades, leaving Arr. philonotis for the last. However, the application of the name was not by default: the light grey colour and scattered fine pileal hairs (Fig. 3e) described in the protologue enabled us to match this name to only one species. The type for A. philonotis, presumed lost, came from a bog close to Berlin, near the North Sea. We selected the closest collection with good material that we sequenced as epitype. It came from a bog near Baden-Württemberg, Germany, a more midcontinental location in the foothills of the Alps, about 500 m asl., a slightly different biome than that of the type location, but we were reassured by finding some of our sequenced specimens in coastal barrens and moors similar to Lasch’s collecting region. This decision seems to be supported by at least three major workers (Favre 1948; Kuyper 1995; Elborne 2008), who apply this epithet to collections with spore measurements similar to ours. That said, of the four, we know Arr. philonotis the least, and have only seen four collections of it in its habitat. Therefore, our descriptions (based only on sequenced specimens directly observed by us) should benefit from augmentation by future observations.

Nomenclatural uncertainty spreads from leading workers to all writings in both professional and amateur journals and books. For example, in his pursuit of the genus Galerina in Auvergne, René-Jacques Bouteville (1998) spent a lot of time in bogs, which resulted in a very nice and compact review of sphagnicolous omphalinas. Much as we, he came up with four species, Omphalina sphagnicola (Berk.) M.M. Moser, O. philonotis (Lasch) Quél., O. oniscus (Fr. nom. sanct.) Quél. and O. fusconigra P.D. Orton. Different from us, he divided them into one scaly capped and three smooth-capped species. His O. sphagnicola seems to fit well with at least the lighter, if not both of our scaly capped species, and his concept of O. fusconigra seems to have a good fit for our Arr. telmatiaea. The remaining two epithets are a bit more difficult to fit to the species as we have outlined them. Current uncertainty in the community is illustrated even more dramatically in an on-line discussion (https://mushroomobserver.org/observer/show_observation/89590, last accessed Mar 31, 2021): for a single collection, knowledgeable mycophiles considered four epithets, weighing three of them almost equally.

We were not aware of sphagnicolous species of Omphalina s. str., so that finding such a species (Fig. 5f, g) was a pleasant surprise. If there is a relationship with Sphagnum, it is facultative, because we find the same species much more frequently in boreal grasslands among low moss on poor soil. Despite the reputed reddish colouration of omphalinas, often this species was not separable macroscopically from a desquamated older Arr. gerardiana (Fig. 3d; 4f), which can appear reddish at times, a non-blackish Arr. telmatiaea (Fig. 3f), or at times even from Arr. philonotis (Fig. 3e; 5a, b). However, it can be separated from these readily by spore size (Fig. 6). So far, this is the only known species of the genus in NL. Our data have been made available to a colleague for phylogenetic type studies of the Omphalina pyxidata complex to identify this species, an undertaking outside the scope of the present study. To aid the reader, a brief description follows.

Larger than the arrhenias, reddish brown, stipitate, about 10–44 mm tall. The cap is 8–40 mm diameter, umbilicate, with downcurved edges quickly becoming plane, then upturned and crenulate with age, transversely striate but hygrophanous and opaque when dry, smooth, covered with sparse, thin, fibrilllose, adpressed, flat scales. Narrow darker radial bands over lamellae and lamellulæ, alternating with wider, lighter intervening bands. Gills are moderately spaced, smooth-edged, deeply decurrent, with 3–5 intervening, small lamellulæ, developing low crossveins beyond maturity, forking very rare; very light off-white, contrasting with the darker stem and cap. Stem 10–38 × 2–7 mm, cylindric, straight concolorous with cap, with sparse white tomentum at its base. Basidiospores measure 6.3–9.1 × 3.6–5.1 μm, ave. 7.8 × 4.4 μm, elliptical, Q = 1.3–2.1, ave. 1.8. Basidia four-spored, clavate, hyaline (Fig. 6). No cystidia. Clamp connections in all tissues. Specimens examined listed in Table 2.

Because we have a large number of collections of sphagnicolous arrhenias from a wide geographic range (Table 3), the likelihood of finding additional species in accessible bogs of Europe or North America is low, but the existence of uncommon sphagnicolous species is possible in remote habitats outside usually surveyed regions. For example, in a report of 32 Nordic sphagnicolous agarics, Lange and Lange (1982) reported two very dark scaly capped sphagnicolous specimens from Greenland that they suspected might represent an unknown species. Spore measurements place them just outside the range of species in our study. As mentioned, we encountered two singleton species of Arrhenia, which we excluded from the current study due to lack of data. After concluding our study, we encountered another singleton in Sphagnum that we were unable to identify (DAO7984941, TUF117659 in Table 1, UDB038438; Voitk and Burzynski 2018). Thus, the possibility of finding...
additional sphagnicolous species in less commonly explored regions may not be exhausted.

Sphagnicolous omphaloid arhenias have been ignored in the era of molecular studies: in 2006, when we first began this investigation, we found only two sequences in GenBank identified with one of the names in our original list, one collection each. This experience demonstrates the major contribution of molecular analysis to taxonomy. Ranking organisms, we use their characters to separate them, but not all characters are equally relevant discriminators at all times. Sometimes cap ornamentation, colour, spore size, or ecology are excellent discriminators between species, while at other times some or all of these characters are irrelevant. Molecular studies identified four species clades, permitting retrospective examination, to learn which characters serve to separate these species and which do not. This requires familiarity with the organisms in their setting. A fresh comparison of protologues and original material to the characters of the identified clades will at times be rewarded with felicitous matches. We hope that this effort to identify the best name to match each clade without conflict, to fix each name with typification, and to circumscribe each species, will provide reliable guidelines for identification, and bring about lasting stability to this relatively small group of interesting fungi.

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Data Availability All specimens are deposited in public fungaria/herbaria (Tables 1, 2, and 3), all sequences in publicly available gene depositories (Tables 1, 2, and 3), and all phylogenies in TreeBase (see text).

Code availability Not applicable.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication All co-authors have read the text and approved its publication, with implicit approval of the institutes where their work was carried out.

Competing interests The authors declare no competing interests.

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