

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 created four clades in *Arrhenia*, three obligate sphagnophiles (two scaly-capped and one smooth-capped) and one facultative (smooth-capped). Nomenclatural review recovered 16 names applied to omphalinoid sphagnicolous taxa in the past. Critical review of these left five as suitable to this group. One scaly 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 *Ag. telmatiaeus* and *Omphalina fusconigra*; we recombined it as *Arr. telmatiaea*. This is the darkest species of the group, with a more northern distribution. The facultative sphagnophile was identified as *Arr. philonotis*, a lighter smooth-capped species also with a more northern distribution. In addition, we 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, and add an informal description of the *Omphalina*. Overall, this study adds new sequences from 82 specimens of sphagnicolous arrhenias to the two existing in GenBank when we began, 11 new sequences of the unidentified species of *Omphalina*, and several other arrhenias.

Introduction

Aim

This study was undertaken to identify the sphagnicolous omphalinoid species of *Arrhenia* Fr. native to the Canadian province of Newfoundland and Labrador (NL). Our interest to learn more about this group was stimulated in part because over 15 years one of these species has been the logo for Foray Newfoundland & Labrador (FNL), the mushroom club of the province, with which three of the four authors are or have been associated.

Definitions

Arrhenia: a genus erected by Fries (1849), belonging to the Hygrophoraceae (Lodge et al. 2014). Currently it contains species of bryophilous fungi with basiomata 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. Obligate sphagnophile: taxon found only with *Sphagnum* L., never separately. Facultative sphagnophile: taxon found in *Sphagnum* with some regularity, but also among other mosses, usually in barren locations where *Sphagnum* is present. Sphagnicolous: taxa regularly found in *Sphagnum*, whether in an obligate or facultative relationship. 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*). Omphalinoid: agaric species with small basiomata having an umbilicate pileus, decurrent gills and central stipe.

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, Cléménçon (1982) – 4, Lange & Lange (1982) – 2, Bigelow (1958, 1985) – 5, Kuyper (1995) – 3, Breitenbach & 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 subalpine peat bogs, followed by seven seasons of daily collecting trips to the alpine zone of the Swiss National Park gave him unsurpassed familiarity with these species in their environment. His work (Favre 1948, 1955) became 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 taxonomy

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 & 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 & von Schweinitz (1805) is the protologue for a new species, something claimed by neither Fries nor von Albertini & von Schweinitz. 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 nostratum, p XIII). *Agaricus tigrinus* is not marked “nobis” and does not appear in the list, making it clear that von Albertini & von Schweinitz 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 (nigricantibus), grey, bristly scales (squamulis pilosis cineris), may suggest a similarity to scaly-capped arrhenias, but Fries clearly described *Ag. affricatus* as a white-capped mushroom, “albidus” in the protologue (Fries 1818) and “albido” in his sanctioning *Systema* (Fries 1821). He did not change this description during his lifetime, and repeated it later with a coloured illustration (Fries 1867), which, he states fits (adumbrat) his *Ag. affricatus*. The illustration shows a basidioma with a snow-white, non-striate pileus with black scales, resembling the current *Lentinus tigrinus*. Both description and image are unsuitable to represent grey-brown and translucent sphagnicolous arrhenias.
6. 1818. *Agaricus incomtus* 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 Schweinitz. 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 2021) 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, Lutzoni, Moncalvo & Vilgalys, 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 “lightly, 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 2021)

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 *Gerronema ericetorum* (= *L. umbellifera*), making this unsuitable name unavailable for sphagnicolous arrhenias.

10. 1865. "*Agaricus affricatus* Berk. & Broome". Berkeley & 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 arrhenias.
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 omphalinoid 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 arrhenias.
12. 1883. *Agaricus telmatiaeus* Berk. & Cooke. This name appeared with the reproduction of an aquarelle by George Masee of his collection near Scarborough, in volume 2 of Cooke's "Illustrations of British Fungi (Hymenomycetes)". The Illustrations appeared in installments, and *Ag. telmatiaeus*, plate 240, appeared Apr–May, 1883 (Stefleu & Cowan 1976). In addition to illustrating the taxon, Masee'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", for which the Illustrations were meant to be an atlas, also appeared in parts; the segment treating *Ag. telmatiaeus* (Cooke 1885) appeared Jan–Apr, 1885 (Stefleu & Cowan 1976). Although the synopsis appeared two 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. & Brooke, 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 Masee's collection from Scarborough, and "from type" on Masee's aquarelle depicting the same collection. Dennis (1948) reviewed *Ag. telmatiaeus* and noted the confusion of names, authors, collections and illustrations. He concluded that Masee's collection from Scarborough was the type specimen for *Ag. telmatiaeus*. The description of this taxon is compatible with a dark smooth-capped sphagnicolous species of *Arrhenia*.
13. 1883. *Agaricus telmaticus* Cooke. The name appeared as entry 1999 in Berkeley and Broome's Notices of British fungi in late 1883, a review of noteworthy finds and publications, which states, "A. (Omphalia) *telmaticus*, Cooke, tab. 240. On *Sphagnum*. This is our *A. affricatus*, which appears not to be the plant of Fries." Placing the period after the plate number, rather than after Cooke, Berkeley and Broome notify the reader that entry 1999 reports a new taxon illustrated on a specific plate (240) in an atlas published by Cooke, not a new species described by Cooke. Failure to recognize this has led to the misinterpretation that Berkeley and Brooke meant to state that Cooke was the author of a taxon named *Ag. telmaticus*. Cooke has never published such an epithet. The cited plate 240 in Cooke's Illustrations shows *Ag. telmatiaeus*, clearly attributing authorship to Berkeley and Cooke. Both epithets cite *Ag. affricatus* as a synonym. The epithet "telmaticus", used by Berkeley and Brooke, is a correct inflectional form of the validly published earlier name for the same species, considered an orthographic variant

by the Code, which rules that the first validly published correct variant be accepted. Were they considered separate names rather than orthographic variants, “telmaticus” would be a superfluous name, to be rejected in favour of the earlier name. Either way, this name is not available.

14. 1883. *Agaricus peculiaris* Britz. 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. Illustrated spores are doubly curved with a Q value 3.4–4.5 (Average 3.8). None of our smooth-capped sphagnicolous arrhenias have spores even close to this size; only one scaly-capped species has spores in this length, but not as prominently doubly curved and with an 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. In an effort to redefine taxa described by Britzelmayr, Bresinsky & Strangl (1974) 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 & Strangl provide no descriptive information about either specimen. Unable to fit the original material to a sphagnicolous *Arrhenia*, we do not consider the name suitable for this group.
15. 1958. *Clitocybe gerardiana* var. *fusca* 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* Orton, and synonymized his variety with Orton’s species. Bigelow’s description remains suitable for scaly-capped sphagnicolous arrhenias.
16. 1960. *Omphalina fusconigra* 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 arrhenias, is the dark, black-brown colouring, not cap texture. He described the cap as “sometimes slightly rugulose or scurfy-flocculose at centre”, in other words an irregularity that was the exception, minimal, and limited. Both wrinkled (rugulose) and flat surfaces can be scaly, scurfy-flocculose, or smooth. Probably because scaly-capped arrhenias are commonly encountered in bogs, the mention of any cap irregularity, no matter how uncommon, limited or inconsequential, encouraged misinterpretation, and *O. fusconigra* became considered a scaly-capped species, synonymized with *Ag. sphagnicola* (also not described as scaly!) and subsequently with the truly scaly *Ag. gerardianus*. We conclude that this name, currently *Arrhenia fusconigra* (P. D. Orton) P.A. Moreau & Courtec., is suitable to apply to dark smooth-capped sphagnicolous arrhenias.

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. telmatiaëus*, 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 basidioma (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 was deposited in TUF (TUF117871). One basidioma from the type collections of *Ag. telmatiaeus*, and one from *O. fusconigra* were sequenced successfully.

Other collections. Study collections were selected from over 150 collections identified to be sphagnicolous omphalinoid arrhenias 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 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).

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. 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 was done in three laboratories. DNA extraction at Bridgewater College (sequences marked with * in Table 1) followed Lickey (2003). DNA extraction at The Field Museum (sequences without a UDB code and not marked with * in Table 1) followed Sulzbacher et al. 2016). DNA extraction at Tartu University (UDB code in Table 1) followed Saar & Voitk (2015).

Table 1

Details of sequenced specimens in order of appearance in Fig. 1, excluding the single NL species in the *Omphalina pyxidata* complex (shown in Tab. 2), and the sphagnicolous arrhenias (shown in Tab. 3)

| Species (as recorded on GenBank deposit) | GB code above, UNITE code below | Primary Herbarium number above, copy below | COUNTRY (Province for Canada) | Reference |
|---------------------------------------------------|---------------------------------------|--------------------------------------------------|-------------------------------------|--------------------------------------------------------------------|
| <i>Omphalina rivulicola</i> | U66451 | | | Lutzoni 1997 |
| <i>Omphalina pyxidata</i> | U66450 | | | Lutzoni 1997 |
| <i>Omphalina pyxidata</i> | UDB0799020 | TUF114379 | ESTONIA | this study |
| <i>Omphalina</i> cf. <i>rivulicola</i> | HQ445617 | | SVALBARD | Bjorbaekmo et al. 2010 |
| <i>Omphalina</i> cf. <i>rivulicola</i> | GU234117 | | SVALBARD | Geml et al. 2012 |
| <i>Omphalina chionophylla</i> | GU234144 | | SVALBARD | Geml et al. 2012 |
| <i>Omphalina chionophylla</i> | MH862276 | | SVALBARD | Vu et al. 2019 |
| <i>Arrhenia epichysium</i> | KC237880 | LE262961 | RUSSIA | Zvyagina et al. 2015 |
| <i>Arrhenia epichysium</i> | U66442 | | | Lutzoni 1997 |
| <i>Arrhenia sphagnicola</i> | GB XXXXXXXXX | DAOMXXXXXXX | CANADA, NL | this study |
| <i>Arrhenia velutipes</i> | UDB034634 | TUF117593 | CANADA, NL | this study |
| <i>Arrhenia philonotis</i> | UDB024403 | M-0155052 | GERMANY | this study |
| <i>Arrhenia sphagnicola</i> | GB XXXXXXXXX | DAOMXXXXXXX | CANADA, NL | this study |
| <i>Arrhenia obscurata</i> | MT967333 UDB024573 | TUF117230 | CANADA, NL | Voitk et al. 2020 |
| <i>Arrhenia obscurata</i> | MT998930 | voucher lost | CANADA, NL | Voitk et al. 2020 |
| <i>Arrhenia acerosa</i> | MT967312 UDB032044 | UPS-F151993 | SWEDEN | Voitk et al. 2020 |
| <i>Arrhenia svalbardensis</i> | MT967358 UDB024589 | O-50446 | SVALBARD | Voitk et al. 2020 |
| <i>Arrhenia auriscalpium</i> | UDB037768 | O-304914 | NORWAY | sequenced as part of the NorBOL project; no associated publication |

| Species (as recorded on GenBank deposit) | GB code above, UNITE code below | Primary Herbarium number above, copy below | COUNTRY (Province for Canada) | Reference |
|---------------------------------------------------|---------------------------------------|--------------------------------------------------|-------------------------------------|--------------------------------------------------------------------------|
| <i>Arrhenia auriscalpium</i> | U66428 | Lutzoni 930804-5, DUKE & O | | Lutzoni 1997 |
| <i>Arrhenia elegans</i> | JF908757 | MCVE-16455 | ITALY | Osmundson et al. 2013 |
| <i>Arrhenia subglobispora</i> | KR606032 | | SWITZERLAND | Senn-Irlet, direct submission (2015) |
| <i>Arrhenia retiruga</i> | MT967340 | TUF117227 | ESTONIA | Voitk et al. 2020 |
| <i>Arrhenia retiruga</i> | UDB036702 | O-21925 | NORWAY | sequenced as part of the NorBOL project; no associated publication |
| <i>Arrhenia lobata</i> | MT967332 | DAOM981256 TUF117633 | CANADA, NL | Voitk et al. 2020 |
| <i>Arrhenia lobata</i> | U66429 | Lutzoni & Lamoure 910824-1, DUKE | FRANCE | Lutzoni 1997 |

The 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 Tabs 1–3).

Phylogenetic analysis. The alignments were performed using L-INS-i strategy as implemented in MAFFT v7.475 (Kato 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. Tab. 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 Tab. 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, are shown in Tab. 3.

Table 2

Specimens of the single NL species in the *Omphalina pyxidata* complex (OPCUS ^a) examined ^b

| CODE: GenBank above, UNITE below | COUNTRY, STATE/PROVINCE, Town, locality above, Coordinates (degree decimal); elevation (m asl) below | Habitat above, Substrate below | Date DD- Mon- YY | Collector above Collection code below | Herbarium code: Main above, copy below |
|----------------------------------------------|---------------------------------------------------------------------------------------------------------------|-----------------------------------------|---------------------------|------------------------------------------------|-------------------------------------------------|
| MH237678 c UDB032178 | 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 |
| 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 UDB032179 | 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 |
| MH473375 f | CANADA, NL, Labrador, Forteau, Overfall Brook trail 51.454297N, 56.947339W; 51 | heath <i>Sphagnum</i> & moss | 08- Sep- 05 | Andrus Voitk 05.09.08.av03 | DAOM744411 |
| MH473374 f | CANADA, NL, Searston Provincial Park 47.835030N, 59.337496W; 2 | heath moss | 05- Jun- 10 | Joe Brazil 10.06.05.av07 | DAOM744410 |
| MH473373 f | CANADA, NL, Searston Provincial Park 47.835030N, 59.337496W; 2 | heath moss | 05- Jun- 10 | Andrus Voitk 10.06.05.av05 | DAOM744409 |
| MH473371 f | CANADA, NL, Gros Morne National Park, trail to Wigwam Lake 9.430075N, 57.744673W; 68 | fen <i>Sphagnum</i> | 01- Nov- 05 | Andrus Voitk 05.11.01.av01 | DAOM744405 |

^a *Omphalina pyxidata* complex, unidentified species—code name given to the single species of *Omphalina* found in NL, mostly 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 at Bridgewater College,

^g Sequence generated by Osmundson et al. (2012)

^h Sequence generated by Landry & Bérubé, direct submission to GenBank, no associated publication.

| CODE: GenBank above, UNITE below | COUNTRY, STATE/PROVINCE, Town, locality above, Coordinates (degree decimal); elevation (m asl) below | Habitat above, Substrate below | Date DD- Mon- YY | Collector above Collection code below | Herbarium code: Main above, copy below |
|----------------------------------------------|---------------------------------------------------------------------------------------------------------------|-----------------------------------------|---------------------------|------------------------------------------------|-------------------------------------------------|
| MN992480 g | CANADA, QC | | 09- Sep- 15 | Renee Lebeuf ANT255- HRL2125 | |
| MN992479 g | 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, E523750, N5689462 | limestone barrens peat | 5- Oct- 16 | Michael Burzynski 16.10.05.av06 | TUF117475 |
| UDB032728 c | CANADA, NL, Labrador, outside Forteau | heath moss | 5- Sep- 05 | Tony Wright GM5-443 | TUF117474 |
| UDB011424 c | ESTONIA | old firepit site | 31- Oct- 07 | Vello Liiv | TUF106200 |
| MH473369 f | CANADA, NL, Ferolle Point 51.020619N, 57.094016W; 6 | heath Sphagnum & moss | 29- Jun- 05 | Andrus Voitk 05.06.29.av01 | DAOM744403 |
| MH473370 f | CANADA, NL, Great Brehat, Great Brehat moor 51.426534N, 55.498613W; 14 | heath <i>Sphagnum</i> & moss | 09- Jun- 10 | Andrus Voitk 10.07.09.av02 | DAOM744404 |

^a *Omphalina pyxidata* complex, unidentified species—code name given to the single species of *Omphalina* found in NL, mostly 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 at Bridgwater College,

^g Sequence generated by Osmundson et al. (2012)

^h Sequence generated by Landry & Bérubé, direct submission to GenBank, no associated publication.

| CODE: GenBank above, UNITE below | COUNTRY, STATE/PROVINCE, Town, locality above, Coordinates (degree decimal); elevation (m asl) below | Habitat above, Substrate below | Date DD- Mon- YY | Collector above Collection code below | Herbarium code: Main above, copy below |
|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------|-----------------------------------------|---------------------------|------------------------------------------------|-------------------------------------------------|
| MH473372 f | CANADA, NL, Gros Morne National Park, Western Brook Pond trail 49.786176N, 57.862653W; 24 | bog <i>Sphagnum</i> | 09- Jun- 07 | Andrus Voitk 07.09.06.av08 | DAOM744406 |
| MH473376 f | CANADA, QC, Saint-Augustin, Saint- Augustin archipelago 51.175867N, 58.479824W; 2 | bog <i>Sphagnum</i> | 24- Jul- 07 | Andrus Voitk 07.07.24.av01 | DAOM744412 |
| ^a <i>Omphalina pyxidata</i> complex, unidentified species—code name given to the single species of <i>Omphalina</i> found in NL, mostly recorded as <i>Omphalina cf. pyxidata</i> . | | | | | |
| ^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 at Bridgwater College, | | | | | |
| ^g Sequence generated by Osmundson et al. (2012) | | | | | |
| ^h Sequence generated by Landry & Bérubé, direct submission to GenBank, no associated publication. | | | | | |

Table 3

Specimens of sphagnicolous arrhenias examined ^a

| GenBank number top UNITE below | Phylogenetic ID ^b | 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 |
|------------------------------------|------------------------------|---------------------------------------------------------------------------------------------------------|--------------------------------|-----------|-----------------------------------------|-----------------------------------------|
| OM422825 ^c UDB038318 | <i>Arrhenia bigelowii</i> | CANADA, NL, Labrador, Battle Harbour, Great Caribou Island, Indian Cove 52.267245°N, 55.629755°W; 42 | bog <i>Sphagnum</i> | 21-Aug-18 | Michael Burzynski TCMB16 | DAOMXXXXXX TUF117647 |
| OM422827 ^c UDB038320 | <i>Arrhenia bigelowii</i> | CANADA, NL, Labrador, Battle Harbour, Great Caribou Island, 52.273339°N, 55.591108°W; 38 | bog <i>Sphagnum</i> | 20-Aug-18 | Michael Burzynski CEMB-01 | DAOMXXXXXX TUF117649 |
| OM422829 ^c UDB038322 | <i>Arrhenia bigelowii</i> | CANADA, NL, Labrador, Battle Harbour, Great Caribou Island, Indian Cove 52.267245°N, 55.629755°W; 42 | bog <i>Sphagnum</i> | 21-Aug-18 | Andrus Voitk TCAV11 | DAOMXXXXXX TUF117651 |
| OM422830 ^c UDB038323 | <i>Arrhenia bigelowii</i> | CANADA, NL, Labrador, Battle Harbour, Great Caribou Island, Indian Cove 52.267245°N, 55.629755°W; 42 | bog <i>Sphagnum</i> | 21-Aug-18 | Maria Voitk TCMV01 | DAOMXXXXXX TUF117652 |
| MH473353 ^d | <i>Arrhenia bigelowii</i> | CANADA, NL, near Great Breat, Great Breat moor 51.426534N, 55.498613W; 14 | bog <i>Sphagnum</i> | 09-Jul-10 | Andrus Voitk 10.07.09.av04 | DAOM744389 |
| MH473349 ^d | <i>Arrhenia bigelowii</i> | CANADA, NL, Trinity East, near Port Rexton, Skewink trail 48.365623N, 53.332913W; 18 | bog <i>Sphagnum</i> | 21-Jun-07 | Andrus Voitk 07.06.21.av02 | DAOM744393 |
| MH473350 ^d | <i>Arrhenia bigelowii</i> | CANADA, NL, near Botwood, New Bay Pond 49.099799N, 55.581375W; 111 | bog <i>Sphagnum</i> | 26-Jun-07 | Andrus Voitk 07.06.26.av01 | DAOM744388 |
| MH473351 ^d | <i>Arrhenia bigelowii</i> | CANADA, QC, Saint-Augustin, Saint-Augustin archipelago 51.175867N, 58.479824W; 2 | <i>Sphagnum</i> | 23-Jul-07 | Andrus Voitk 07.07.23.av07 | DAOM744395 |

| GenBank number top UNITE below | Phylogenetic ID ^b | 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 |
|------------------------------------|-------------------------------------------|-----------------------------------------------------------------------------------------------------|--------------------------------|------------------|-----------------------------------------|-----------------------------------------|
| MH473352 ^d | <i>Arrhenia bigelowii</i> | CANADA, QC, Saint-Augustin, Saint-Augustin archipelago 51.175867N, 58.479824W; 2 | bog <i>Sphagnum</i> | 23-Jul-07 | Andrus Voitk 07.07.23.av09 | DAOM744394 |
| MH473348 ^{d, e} | <i>Arrhenia bigelowii</i> holotype | CANADA, NL, Rocky Harbour, Rocky Harbour bog 49.577694N, 57.898916W; 35 | bog Sphagnum | 05-Jul-04 | Andrus Voitk 04.07.05.av03 | DAOM744391 |
| MH473347 ^d | <i>Arrhenia bigelowii</i> | CANADA, NL, Labrador, near Red Bay Tracy's Hill 51.72972N, 56.447783W; 138 | bog <i>Sphagnum</i> | 15-Jun-05 | Andrus Voitk 05.06.15.av01 | n/a ^e |
| MH198227 ^c UDB034637 | <i>Arrhenia bigelowii</i> | SWEDEN, Sydbillingens Nature Reserve, Sättingen | | 19-Jun-86 | Anders Dahlberg 86018 | GB-0072229 |
| MH198189 ^c UDB024397 | <i>Arrhenia bigelowii</i> | FINLAND, Pohjois-Savo, Vehmersalmi, Rytökylä | | 26-Sep-93 | Ilkka Kytövuori 92-147 | H6057135 |
| MH198188 ^c UDB024396 | <i>Arrhenia bigelowii</i> | FINLAND, Pohjois-Häme, Virrat, Hauhuu | | 05-Aug-90 | Ilkka Kytövuori 90-133 | H6057146 |
| MH198195 ^c UDB024405 | <i>Arrhenia bigelowii</i> | GERMANY, Bayern, Garmisch-Partenkirchen, Saulgrub | | 13-Jun-96 | Christoph Johannes Hahn | M-0276634 |
| MH198192 ^c UDB024401 | <i>Arrhenia bigelowii</i> | SWEDEN, Södermanland, Vårdinge, Sjuendaskogen, between St. and L. Alsjön | | 09-Aug-94 | Klas Jaederfeldt | S-F277529 |
| MH198190 ^c UDB024398 | <i>Arrhenia bigelowii</i> | SWEDEN, Uppland Hållnäs par., Lake Fräkensjön (= 4 km N of Hållnäs) | | 06-Aug-83 | Nils Lundquist 14499 | S-F277532 |
| MH198219 ^c UDB034625 | <i>Arrhenia bigelowii</i> | CANADA, NL, Gros Morne National Park, bog at foot of Gros Morne Mt. 49.577694N, 57.898916W; 35 | bog <i>Sphagnum</i> | 12-Aug-08 | Andrus Voitk 08.08.12.av05 | DAOM744390 TUF117583 |

| GenBank number top UNITE below | Phylogenetic ID ^b | 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 |
|------------------------------------|-----------------------------------------------------------------|---------------------------------------------------------------------------------------------------------|--------------------------------|-----------|-----------------------------------------|-----------------------------------------|
| MH198220 ^c UDB034626 | <i>Arrhenia bigelowii</i> | CANADA, NL, Labrador, Battle Harbour, Great Caribou Island, Indian Cove 52.2668N, 55.648W; 17 | bog <i>Sphagnum</i> | 19-Aug-08 | Andrus Voitk BH-018 (IC57) | TUF117584 |
| MH198204 ^c UDB032052 | <i>Arrhenia bigelowii</i> | GERMANY, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald | | 05-Jul-05 | Doris Laber | KR-0003833 |
| MH198205 ^c UDB032053 | <i>Arrhenia bigelowii</i> | GERMANY, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald | | 18-Jul-84 | Doris Laber | KR-0004262 |
| MH198207 ^c UDB032056 | <i>Arrhenia bigelowii</i> | GERMANY, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald | | 19-Aug-06 | Doris Laber | KR-0004519 |
| MH198206 ^c UDB032054 | <i>Arrhenia bigelowii</i> | GERMANY, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald | | 08-Sep-03 | Doris Laber | KR-0004576 |
| OM422833 ^c UDB038353 | <i>Clitocybe gerardiana</i> var. <i>fusca</i> varietal holotype | USA, MICH, Luce co., Pike Lake | bog Sphagnum | 11-Sep-53 | A. H. Smith 42574 | MICH10143 TUF117871 |
| OM422824 ^c UDB038317 | <i>Arrhenia bigelowii</i> | CANADA, NL, Labrador, Battle Harbour, Great Caribou Island, 52.273339°N, 55.591108°W; 38 | bog <i>Sphagnum</i> | 20-Aug-18 | Michael Burzynski CEMB-02 | DAOMXXXXXX TUF117646 |
| OM422832 ^c UDB038325 | <i>Arrhenia bigelowii</i> | CANADA, NL, Labrador, Battle Harbour, Great Caribou Island, Indian Cove 52.267245°N, 55.629755°W; 42 | barrens, peat | 21-Aug-18 | Michael Burzynski TCMB09 | DAOMXXXXXX TUF117657 |
| MH473354 ^d | <i>Arrhenia bigelowii</i> | CANADA, NL, near Stephenville 48.542358N, 58.118079W; 24 | bog <i>Sphagnum</i> | 08-Aug-07 | Andrus Voitk 07.08.08.av02 | DAOM744392 |

| GenBank number top UNITE below | Phylogenetic ID ^b | 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 |
|------------------------------------------------|------------------------------|-----------------------------------------------------------------------------------------------------|--------------------------------|-----------|-----------------------------------------|-----------------------------------------|
| OM422835 ^c g UDB0802694 | <i>Arrhenia bigelowii</i> | CANADA, NL, Stephenville Crossing, 48.516017N, 58.433798W; 16 | bog <i>Sphagnum</i> | 17-Aug-10 | Andrus Voitk 10.08.17.av01 | TUF117886 |
| MH198199 ^c UDB032042 | <i>Arrhenia gerardiana</i> | GERMANY, Fürstenfeldbruck | | 24-Jun-73 | Andreas Bresinsky | M-0276635 |
| MH198191 ^c UDB024399 | <i>Arrhenia gerardiana</i> | SWEDEN, Dalarna, Orsa par., Tunturi, NE of Mt. Stora (22 km N of Skattungbyn) | | 10-Aug-93 | Nils Lundquist 19520 | S-F277528 |
| MH473366 ^d | <i>Arrhenia gerardiana</i> | CANADA, NL, Gros Morne National Park, Western Brook Pond trail 49.786176N, 57.862653W; 24 | bog <i>Sphagnum</i> | 15-Jun-06 | Andrus Voitk 06.06.15.av04 | DAOM744373 |
| MH473357 ^d MH473358 ^d | <i>Arrhenia gerardiana</i> | CANADA, NL, Cheesman Park 47.632104N, 59.256736W; 3 | bog <i>Sphagnum</i> | 15-Jul-04 | Andrus Voitk 04.07.15.av01 | DAOM744371 |
| MH473359 ^d | <i>Arrhenia gerardiana</i> | CANADA, NL, Rocky Harbour, Rocky Harbour bog 49.577694N, 57.898916W; 35 | bog <i>Sphagnum</i> | 03-Jul-05 | Andrus Voitk 05.07.03.av01 | DAOM744376 |
| MH473355 ^d | <i>Arrhenia gerardiana</i> | CANADA, NL, Rocky Harbour, Rocky Harbour bog 49.577694N, 57.898916W; 35 | bog <i>Sphagnum</i> | 03-Jul-05 | Andrus Voitk 05.07.03.av02 | DAOM744377 |
| MH473367 ^d | <i>Arrhenia gerardiana</i> | CANADA, NL, Rocky Harbour, Rocky Harbour bog 49.577694N, 57.898916W; 35 | bog <i>Sphagnum</i> | 03-Jul-05 | Andrus Voitk 05.07.03.av03 | DAOM744375 |
| MH473365 ^d | <i>Arrhenia gerardiana</i> | CANADA, NL, near Gillams, Gillams bog 49.011140N, 58.066273W; 103 | bog <i>Sphagnum</i> | 16-Jul-08 | Andrus Voitk 08.07.16.av01 | DAOM744372 |
| MH473361 ^d | <i>Arrhenia gerardiana</i> | CANADA, QC, Saint-Augustin, Saint-Augustin archipelago 51.175867N, 58.479824W; 2 | bog <i>Sphagnum</i> | 24-Jul-07 | Andrus Voitk 07.07.24.av02 | DAOM744387 |

| GenBank number top UNITE below | Phylogenetic ID ^b | 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 |
|--------------------------------------------|------------------------------------|-----------------------------------------------------------------------------------------------------|--------------------------------|----------------|-----------------------------------------|-----------------------------------------|
| MH47335 ^d | <i>Arrhenia gerardiana</i> | CANADA, QC, Saint-Augustin, Saint-Augustin archipelago 51.175867N, 58.479824W; 2 | bog <i>Sphagnum</i> | 23-Jul-07 | Andrus Voitk 07.07.23.av02 | DAOM744386 |
| MH473363 ^d | <i>Arrhenia gerardiana</i> | CANADA, QC, Saint-Augustin, Saint-Augustin archipelago 51.175867N, 58.479824W; 2 | bog <i>Sphagnum</i> | 21-Jul-07 | Andrus Voitk 07.07.21.av01 | DAOM744384 |
| MH473360 ^d | <i>Arrhenia gerardiana</i> | CANADA, NL, Rocky Harbour, Rocky Harbour bog 49.577694N, 57.898916W; 35 | bog <i>Sphagnum</i> | 15-Jun-06 | Andrus Voitk 06.06.15.av02 | DAOM744378 |
| MH473362 ^d | <i>Arrhenia gerardiana</i> | CANADA, QC, Saint-Augustin, Saint-Augustin archipelago 51.175867N, 58.479824W; 2 | bog <i>Sphagnum</i> | 23-Jul-07 | Andrus Voitk 07.07.23.av01 | DAOM744385 |
| MH198183 ^c UDB024327 | <i>Arrhenia gerardiana</i> epitype | USA, New York, Essex Co., North Elba, Mount Marcy | bog Sphagnum | undated | Charles Peck | NYSd4725.1 |
| MH198221 ^c UDB034627 | <i>Arrhenia gerardiana</i> | CANADA, NL, Labrador, Battle Harbour, Great Caribou Island, Indian Cove 52.2668N, 55.648W; 17 | bog <i>Sphagnum</i> | 19-Aug-08 | Maria Voitk BH-020 (IC54) | DAOM744382 TUF117585 |
| MH198222 ^c UDB034628 | <i>Arrhenia gerardiana</i> | CANADA, NL, Labrador, Battle Harbour, Great Caribou Island, Indian Cove 52.2668N, 55.648W; 17 | bog <i>Sphagnum</i> | 19-Aug-08 | Anne Marceau BH-022 (IC55) | TUF117586 |
| MH198223 ^c UDB034629 | <i>Arrhenia gerardiana</i> | CANADA, NL, Labrador, Battle Harbour, Great Caribou Island, Indian Cove 52.2668N, 55.648W; 17 | bog <i>Sphagnum</i> | 19-Aug-08 | Maria Voitk BH-021 (IC56) | TUF117587 |

| GenBank number top UNITE below | Phylogenetic ID ^b | 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 |
|------------------------------------------|------------------------------|------------------------------------------------------------------------------------------------------|--------------------------------|-----------|-----------------------------------------|-----------------------------------------|
| MH198224 ^c UDB034631 | <i>Arrhenia gerardiana</i> | CANADA, NL, Rocky Harbour, Rocky Harbour bog 49.577694N, 57.898916W; 35 | bog <i>Sphagnum</i> | 04-Jul-17 | Michael Burzynski 17.07.04.av02 | DAOM744379 TUF117590 |
| MH198225 ^c UDB034632 | <i>Arrhenia gerardiana</i> | CANADA, NL, Rocky Harbour, Rocky Harbour bog 49.577694N, 57.898916W; 35 | bog <i>Sphagnum</i> | 05-Jul-17 | Michael Burzynski 17.07.05.av04 | DAOM744380 TUF117591 |
| MH198226 ^c UDB034633 | <i>Arrhenia gerardiana</i> | CANADA, NL, Rocky Harbour, Rocky Harbour bog 49.577694N, 57.898916W; 35 | bog <i>Sphagnum</i> | 05-Jul-17 | Michael Burzynski 17.07.05.av05 | DAOM744381 TUF117592 |
| OM422826 ^c UDB038319 | <i>Arrhenia gerardiana</i> | CANADA, NL, Labrador, Battle Harbour, Great Caribou Island, 52.273339°N, 55.591108°W; 38 | bog <i>Sphagnum</i> | 20-Aug-18 | Andrus Voitk CEAV-03 | DAOMXXXXXX TUF117648 |
| OM422831 ^c UDB038324 | <i>Arrhenia gerardiana</i> | CANADA, NL, Labrador, Battle Harbour, Great Caribou Island, Indian Cove 52.267245°N, 55.629755°W; 42 | bog <i>Sphagnum</i> | 21-Aug-18 | Michael Burzynski TCMB-04 | DAOMXXXXXX TUF117653 |
| MH473364 ^d | <i>Arrhenia gerardiana</i> | CANADA, NL, Gros Morne National Park, Western Brook Pond trail 49.786176N, 57.862653W; 24 | bog <i>Sphagnum</i> | 31-Aug-08 | Andrus Voitk 08.08.31.av02 | DAOM744374 |
| MH198218 ^c UDB034624 | <i>Arrhenia gerardiana</i> | CANADA, Labrador, W of Konrad Brook Pond 56.139413N, 62.730548W; 50 | bog <i>Sphagnum</i> | 28-Jul-08 | Esteri Ohenoja KL-014 (K42) | DAOM744383 TUF117581 |
| OM422828 ^c UDB038321 | <i>Arrhenia gerardiana</i> | CANADA, NL, Labrador, Battle Harbour, Great Caribou Island, 52.273339°N, 55.591108°W; 38 | bog <i>Sphagnum</i> | 20-Aug-18 | Maria Voitk CEMV-02 | DAOMXXXXXX TUF117650 |
| OM422836 ^c g UDB0802695 | <i>Arrhenia gerardiana</i> | CANADA, NL, near Stephenville | bog <i>Sphagnum</i> | 13-Jul-10 | Andrus Voitk 10.07.13.av06 | TUF117887 |

| GenBank number top UNITE below | Phylogenetic ID ^b | 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 |
|--------------------------------------------|--------------------------------------|-----------------------------------------------------------------------------------------------------|-------------------------------------|------------------|-----------------------------------------|-----------------------------------------|
| n/a ^{g,h} | <i>Agaricus gerardianus</i> holotype | USA, New York | bog Sphagnum | undated | Charles Peck | NYSf4339.1-4 |
| MH198198 ^c UDB32176 | <i>Arrhenia philonotis</i> | CANADA, NL, Labrador, L'Anse Amour 51.470074N, 56.870960W; 2 | heath moss | 16-Aug-08 | Esteri Ohenoja LS-008 (AD-14) | TUF117360 |
| MH198187 ^c UDB024395 | <i>Arrhenia philonotis</i> | FINLAND, Uusimaa, Nurmijärvi, Klaukkala | | 08-Jul-84 | Pirkko Askola, Tauno Toivonen 1413 | H6057134 |
| MH198203 ^c UDB032501 | <i>Arrhenia philonotis</i> epitype | GERMANY, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald | | 29-Jul-84 | Doris Laber | KR-0003880 |
| MH198202 ^c UDB032050 | <i>Arrhenia philonotis</i> | GERMANY, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald | | 18-Aug-90 | Doris Laber | KR-0004132 |
| MH198194 ^c UDB024404 | <i>Arrhenia philonotis</i> | GERMANY, Oberbayern, Moor am Eßsee | | 28-Jun-58 | J. Poelt | M-0276633 |
| MH491520 ⁱ | <i>Arrhenia philonotis</i> | CANADA, NL, Labrador, Konrad Brook 56.278381N, 62.933697W; 517 | bog <i>Sphagnum</i> | 30-Jul-08 | Michael Burzynski KL-013 (T13) | DAOM744400 |
| MH491521 ⁱ | <i>Arrhenia philonotis</i> | CANADA, NL, Labrador, L'Anse Amour 51.470074N, 56.870960W; 2 | bog <i>Sphagnum</i> | 15-Aug-08 | Maria Voitk LS-010 (LAT4) | n/a ^j |
| MH198197 ^c UDB032175 | <i>Arrhenia philonotis</i> | CANADA, NL, Labrador, Konrad Brook 56.278381N, 62.933697W; 517 | bog <i>Sphagnum</i> & moss | 30-Aug-08 | Andrus Voitk KL-015 (T3) | DAOM744401 TUF117359 |
| U66449 ^k | <i>Arrhenia philonotis</i> | GREENLAND | | | François Lutzoni (1997) | |
| MH473368 ^d | <i>Arrhenia philonotis</i> | NORWAY, near Tromsø, Kaldfjord 69.679009N, 18.737086E; 75 | fen, moss and <i>Sphagnum</i> | 06-Jul-08 | Andrus Voitk 08.07.06.av01 | DAOM744402 |

| GenBank number top UNITE below | Phylogenetic ID ^b | 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 |
|------------------------------------|--------------------------------------|-----------------------------------------------------------------------------------------------------|--------------------------------|-------------|-----------------------------------------|-----------------------------------------|
| OM422834 ^c UDB039743 | <i>Agaricus telmatiaeus</i> holotype | UK, ENGLAND, Yorkshire County, Scarborough | Sphagnum | 08-Nov-1882 | G.E. Masee | NY12555 |
| MH198211 ^c UDB032770 | <i>Arrhenia telmatiaea</i> | GERMANY, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald | | 05-Oct-86 | Doris Laber | KR-0004131 |
| MH198201 ^c UDB032049 | <i>Arrhenia telmatiaea</i> | GERMANY, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald | | 03-Oct-04 | Doris Laber | KR-0004167 |
| MH198200 ^c UDB032048 | <i>Arrhenia telmatiaea</i> | GERMANY, Baden-Württemberg, Schwarzwald, Breisgau-Hochschwarzwald | | 10-Oct-07 | Doris Laber | KR-0004666 |
| MH198196 ^c UDB032174 | <i>Arrhenia telmatiaea</i> | CANADA, NL, L'Anse aux Meadows 51.594895N, 55.533285W; 6 | bog <i>Sphagnum</i> | 18-Sep-12 | Andrus Voitk GNP-064 | TUF117357 |
| MH198210 ^c UDB032723 | <i>Arrhenia telmatiaea</i> | CANADA, NL, Labrador, Trans Labrador Highway 52.899521N, 57.161205W; 374 | bog <i>Sphagnum</i> | 14-Sep-16 | Maria Voitk 16.09.14.av01 | DAOM744398 TUF117458 |
| MH198214 ^c UDB034619 | <i>Arrhenia telmatiaea</i> | ESTONIA, Tartu Co., Puhja Comm. | | 16-Oct-86 | Kuulo Kalamees | TAAM143530 |
| MH198228 ^c UDB034638 | <i>Arrhenia telmatiaea</i> | SWEDEN, Västra Götaland Co., Essunga Comm., Bäreberg | | 02-Sep-89 | Leif & Anita Stridvall LAS89/024 | GB-0065942 |
| MH198184 ^c UDB024392 | <i>Arrhenia telmatiaea</i> | FINLAND, Varsinais-Suomi, Vihti, Iso Sammakko | | 08-Oct-96 | Ilkka Kytövuori 96-1308 | H6034872 |
| MH198186 ^c UDB024394 | <i>Arrhenia telmatiaea</i> | FINLAND, Etelä-Häme, Lempäälä, Hietaniemi | | 12-Sep-87 | Pertti Salo 8133 | H6042077 |
| MH198185 ^c UDB024393 | <i>Arrhenia telmatiaea</i> | FINLAND, Uusimaa, Kirkkonummi, Väransby | | 26-Sep-93 | Ilkka Kytövuori 93-1524 | H6057157 |

| GenBank number top UNITE below | Phylogenetic ID ^b | 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 |
|------------------------------------|--------------------------------------|------------------------------------------------------------------------------------------------------|--------------------------------|-----------|-----------------------------------------|-----------------------------------------|
| MH198182 ^c UDB024581 | <i>Omphalina fusconigra</i> holotype | UK, SCOTLAND, South Perthshire, Blair Drummond | Sphagnum | 28-Sep-57 | J. Grainger | K(M)98588 |
| MH198193 ^c UDB024402 | <i>Arrhenia telmatiaea</i> | GERMANY, Bayern, Garmisch-Partenkirchen, Fügsee | | 22-Oct-95 | Christoph Johannes Hahn | M-0276632 |
| MH198213 ^c UDB034618 | <i>Arrhenia telmatiaea</i> | ESTONIA, Ida-Viru Co., Sirtsu swamp | | 01-Oct-95 | Tõnu Ploompuu | TAAM142868 |
| MH198216 ^c UDB034621 | <i>Arrhenia telmatiaea</i> | ESTONIA, Pärnu Co., Nigula bog | | 10-Oct-88 | Kuulo Kalamees, Mall Vaasma | TAAM144086 |
| MH198217 ^c UDB034622 | <i>Arrhenia telmatiaea</i> | ESTONIA, Tartu Co., Ahunapalu | | 09-Nov-91 | Kuulo Kalamees | TAAM145308 |
| MH198215 ^c UDB034620 | <i>Arrhenia telmatiaea</i> | ESTONIA, Ida-Viru Co., Sirtsu swamp | | 06-Oct-96 | Tõnu Ploompuu | TAAM147228 |
| MH198212 ^c UDB034617 | <i>Arrhenia telmatiaea</i> | CANADA, NL, Labrador, Trans Labrador Highway near Red Bay 51.749723N, 56.420208W; 27 | bog <i>Sphagnum</i> | 07-Sep-05 | Tony Wright 05.09.07.av01 | DAOM744399 TUF117580 |
| U66453 ^k | <i>Arrhenia telmatiaea</i> | GREENLAND, Disco | | | François Lutzoni | |
| MH198229 ^c UDB034639 | <i>Arrhenia telmatiaea</i> | SWEDEN, Västra Götaland Co., Trollhättan Comm., Björndalen | | 11-Oct-97 | Leif & Anita Stridvall LAS97/113 | GB-0065958 |
| MH198208 ^c UDB032193 | <i>Arrhenia telmatiaea</i> | CANADA, NL, Labrador, near Northwest River, Goose Bay Ski Club, Loppet trail 53.33853N, 60.4497W; 44 | bog <i>Sphagnum</i> | 10-Sep-16 | Chris Deduke GBHV16B-253 | DAOM744396 TUF117457 |
| MH198209 ^c UDB032194 | <i>Arrhenia telmatiaea</i> | CANADA, NL, Labrador, Red Bay, Saddle Island 51.724588N, 56.426100W; 24 | bog <i>Sphagnum</i> | 08-Sep-05 | Andrus Voitk 05.09.08.av02 | DAOM744397 TUF117459 |
| | <i>Arrhenia telmatiaea</i> | CANADA, NL, Cape Freels Cemetery | barrens <i>Sphagnum</i> | 22-Sep-21 | Bill Bryden 21.09.22.av01 | TUF117940 |

| GenBank number top UNITE below | Phylogenetic ID ^b | 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 |
|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------|-----------------------------------------------------------------------------------------------------|--------------------------------|-----------|-----------------------------------------|-----------------------------------------|
| | <i>Arrhenia telmatiaea</i> | CANADA, NL, Cape Freels | barrens <i>Sphagnum</i> | 22-Sep-21 | Andrus Voitk 21.09.22.av02 | TUF117941 |
| | <i>Arrhenia telmatiaea</i> | CANADA, NL, Cape Freels | barrens <i>Sphagnum</i> | 22-Sep-21 | Greg Thorn 21.09.22.av03 | TUF117942 |
| ^a Arranged by species in alphabetical order. Within each species, collections appear in order of appearance in Fig. 2, followed, where applicable, by sequenced specimens not in Fig. 2, and one unsequenced specimen. | | | | | | |
| ^b Type collections, in boldface, bear their basionym, all others identified by their current names. | | | | | | |
| ^c Sequence generated at Tartu University. | | | | | | |
| ^d Sequence generated at Bridgwater College | | | | | | |
| ^e Logoimage for Foray Newfoundland & Labrador. | | | | | | |
| ^f Specimen all used up in sequencing. | | | | | | |
| ^g Sequence not shown in Fig. 2. | | | | | | |
| ^h Specimen failed to yield amplifiable DNA. | | | | | | |
| ⁱ Sequence generated at the Field Museum, | | | | | | |
| ^j Collection lost in transit on return from sequencing. | | | | | | |
| ⁱ Sequence generated by Lutzoni (1997). | | | | | | |

Phylogeny

The studied collections produced two singleton collections and four clades within *Arrhenia*, as well as one clade that fell in *Omphalina*, code named here “OPCUS”, acronym for *Omphalina pyxidata* complex, unidentified species (Figs. 1, 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. telmatiaea* (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, both identified in the field as “*Omphalina sphagnicola*” and labeled ‘sphagnicola’ on Fig. 1, fell elsewhere within *Arrhenia*. The name was one primarily, but not exclusively, used for scaly-capped sphagnicolous arrhenias at the time; because we have very little tissue left, and lack notes or photographs for these collections, including whether they were

sphagnicolous or scaly, and have not collected them again on return trips to the same sites, we show them but do not treat them here.

Macromorphology

Phylogenetic clades correlated with morphological characters. Both species in the earlier diverging lineage have pilei usually under 20 mm in diameter, covered to a various degree by radially arranged darkening scales with upturned tips (Fig. 3a–c; 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 *Arr. bigelowii* specimens undergo a marked darkening reaction (Fig. 4b, d); the species as a whole may be a little darker than *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; 4f), possibly through loss of the outer pileipellis layer, making such specimens difficult to distinguish from similar smooth-capped taxa, particularly OPCUS. The two smooth-capped species (Fig. 5) in the more derived lineage, have mature cap diameters over 20 mm, at times reaching over 35. Rudimentary outlines of similar scales can be seen in the pileipellis of *Arr. telmatiaea* (Fig. 3f, g), which remain adpressed without tips rising up. 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 visible with magnification (Fig. 3e).

The 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 is well seen 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 protologue for *Arr. philonotis* fits the specimens in its clade (Fig. 5a, b). Most of the time these two smooth-capped species are relatively easy to separate because one has very dark caps, the other lighter, but both have a wide spectrum of darkness (Fig. 3f, g for *Arr. telmatiaea* and 5 a, b for *Arr. philonotis*), making confusion possible. OPCUS (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. 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 $7.3 \times 4.7 \mu\text{m}$, separating it from *Arr. philonotis*, averaging $8.7 \times 5.6 \mu\text{m}$, 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 as 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 incrustated 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 was subtle and required 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 obligate 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 other smooth-capped species, *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. OPCUS was collected from bogs with *Sphagnum* (Fig. 5g) or heaths and moors with other mosses, but was most common in grasslands with low moss (Fig. 5f). All four species of *Arrhenia* were distributed through 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 seemed to extend throughout the province. OPCUS shared the same distribution with the scaly-capped species in NL, and matching GenBank sequences (not shown in our tree), confirm its presence in Europe.

Taxonomy

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

MycoBank MB827069

Typification: CANADA, NL, Rocky Harbour bog, 49.577694°N, 57.898916°W, 35 m asl, bog in *Sphagnum*, 5 Jul 2005, leg. *Andrus Voitek* 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. Scaly-capped obligate sphagnophilic denizen of temperate to subarctic raised bogs, pileus usually under 20 mm diameter, occasionally darkens. 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 diagnostic ITS sequence.

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, translucently striate, smooth, but covered with somewhat

concentric radially arranged scales with darker brown, burr-like, uplifted, centripetally narrowing ends. Narrow brown radial bands over lamellae and lamellulae, alternating with wider, tan intervening bands; the latter become sulcate with time, giving the cap a radially ribbed appearance. Rim of edge 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: 2–5 × 10–23 mm, cylindrical, straight; becoming somewhat hollow; minutely tomentose, glabrescent with age, brown, sparse white tomentum at base. Context: whitish, odor 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 incrustated brown pigment, superficial layers forming small plates on the cell surface (Fig. 7a). Scale tips end with gently swollen rounded unpigmented clear cells (Fig. 7e, f). 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 oxycoccos* L., *V. macrocarpon* Aiton, *Rubus chamaemorus* L., *Empetrum nigrum* L., *Andromeda polifolia* L., and various bog orchids, reeds and grasses, June–Sept, most plentiful in July. May be found in the same bog at the same time as *Arr. gerardiana*.

Distribution: Known from North America and Europe; in NL found throughout the province, more common on the Island.

Additional specimens examined: See Table 3.

Comments: Often indistinguishable from *Arr. gerardiana*: darkening reaction often absent and pileus becomes more plane with age. Although statistical analysis shows that the spore size difference is highly significant (for Q, $t = -6.31$; d.f. = 788; $p < 0.001$), spore sizes of the two species overlap sufficiently to make this character useful only when the averages occupy the extremes of their respective range. We elected to describe it as a new species because we wished to provide a fully examined and robust type collection for posterity. Bigelow (1958) described the growth pattern as “scattered”, typical of scaly-capped sphagnicolous arrhenias, whose individual organisms usually produce 1–2 fruiting bodies at any one time, and seldom more than six. Smith’s holotype collection of *C. gerardiana* var. *fusca* consists of more than 30 basidiomata, and must sample several individual organisms. Because both *Arr. bigelowii* and *Arr. gerardiana* are macro- and micromorphologically very similar, known to occur in the same bog at the same time, a multi-individual collection increases the likelihood of containing both species. We have not examined the entire collection, but only a cap fragment, from which tissue has been removed for both microscopy and molecular studies. This seems inadequate to designate as lectotype, when an abundance of tissue remains in the holotype for the variety, and typifying the species with an ample and fully examined collection seems the more prudent choice. In addition, given the considerable confusion caused by the name “fusconigra” in the past, avoiding a name from the same root seems advantageous, all the more appropriate because 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) gerardianus* Peck, Bull. Buffalo Soc. Nat. Sci. 1: 46. 1873.

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 $6.8\text{--}12.4 \times 3.4\text{--}5.1 \mu\text{m}$ (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 $24 \times 7 \mu\text{m}$. 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 $7.9\text{--}11.5 \times 3.3\text{--}4.2 \mu\text{m}$ (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 $24 \times 7 \mu\text{m}$. 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 edges, but rarely assuming an inverted bowl shape, becoming plane, then crenulate with age, translucently striate, smooth, but covered with somewhat concentric radially arranged scales with darker brown, burr-like, uplifted, narrow distal ends. These scales seem to recede with age, and occasional very mature specimens with large caps may have no distinctive scales (Fig. 3d; 4f). Narrow brown radial bands over lamellae and lamellulae, alternating with wider, tan intervening bands; the latter become minimally sulcate with time. Rim of edge 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: 2–5 × 10–25 mm, cylindric, straight; becoming somewhat hollow; minutely tomentose, which may disappear with age, brown with sparse white tomentum at base. Context: whitish, odor unremarkable.

Micromorphology: Basidiospores (443 spores, 20 basiomata, 17 collections, 3 observers) $6.2\text{--}12.9 \times 2.8\text{--}5.6 \mu\text{m}$, ave. $8.9 \times 4.2 \mu\text{m}$, 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 incrustated brown pigment, superficial layers forming small plates on the cell surface (Fig. 7b). Scale tips end with gently swollen rounded unpigmented 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 smooth-capped sphagnicolous omphalinoids. This character may be lost in very few overly mature and large specimens, requiring microscopic examination to distinguish them from *Arr. philonotis*, OPCUS, or even lighter-coloured *Arr. telmatiaea*. Differs from *Arr. bigelowii* by its more plane pilei, by not turning grey to black in response to unknown stimuli, and shorter spores; these characters are not always evident.

Peck (1873) mentioned two collections in his description of *Agaricus gerardianus* (NYSf 1339 and NYSf 1340), which become syntypes because he did not designate either as holotype. NYSf 1340 is presumed lost; we designated the remaining collection (NYSf 1339.1–4) with its four basiomata, as lectotype for the species. Comparison of spore size has allowed us to conclude that the lectotype is conspecific with collection NYSd 4725, identified by Peck as *Ag. gerardianus*. Because the lectotype did not yield DNA, but NYSd 4725 did, we designated the latter as epitype for *Arrhenia gerardiana*, thus defining the clade in which it resides as that species.

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

MycoBank MB374174

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. Lober*, (**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 $7.7\text{--}10.4 \times 5.2\text{--}7.6 \mu\text{m}$ (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 $24 \times 7 \mu\text{m}$. Cap structure not examined.

Macromorphology (Fig. 3e; 5a,b): Basidioma: Brown, stipitate, 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. Rim of edge 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: 2–5 × 10–25 mm, cylindrical, straight; becoming somewhat hollow; minutely tomentose, glabrescent, brown with sparse white tomentum at base. Context: whitish, odor unremarkable.

Micromorphology: Basidiospores (102 spores, 5 basidiomata, 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). 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 incrustated 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 oxycoccos*, *V. macrocarpon*, *Rubus chamaemorus*, *Empetrum 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. telmatiaea* by its lighter hue and from OPC by its greyish rather than reddish brown hues and broader spores.

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

MycoBank MB842881

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

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

Basionym: *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!**).

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, floccules 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. Rim of edge 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: 2–6 × 10–28 mm, cylindric, straight; becoming somewhat hollow; minutely tomentose, glabrescent, concolorous with pileus with sparse white tomentum at base. Context: lighter brown, odor 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; mostly four-spored with occasional two-spored; clavate, hyaline. No pleuro-, cheilo- or caulocystidia, but terminal hyphal cells protrude from stipe as small hairs. Pielipellis a cutis with thin-walled, clamped hyphae, 3.5–9.0 µm wide, hyaline to brownish, with sparsely to moderately incrustated 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 oxycoccos*, *V. macrocarpon*, *Rubus chamaemorus*, *Empetrum 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, the Great Northern Peninsula, and the northern east coast.

Specimens examined: See Table 3.

Comments: Its obviously and relatively even dark colour distinguishes it from the other smooth-capped sphagnicolous species, *Arr. philonotis*, but on occasion may be more dark brown than near-black, requiring microscopic examination to confirm identification. *Omphaliaster borealis* (M. Lange & Skifte) 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).

OPCUS (Omphalina pyxidata complex, unidentified species) Fig. 5f,g

Macromorphology: Basidioma: Brown, stipitate, about 10–44 mm tall, with various mosses in grassland, moor, fen, as well as bog with *Sphagnum*. Pileus: 8–40 mm diameter, umbilicate, downcurved edges quickly becoming plane, then upturned and crenulate with age, translucently striate but hygrophanous and opaque when dry, smooth, covered with sparse, thin, fibrillose, adpressed, flat scales. Narrow brown or reddish brown radial bands over lamellae and lamellulae, alternating with wider, tan intervening bands. Red more noticeable if opaque. Lamellae: moderately spaced, smooth-edged, deeply decurrent, with 3–5 intervening, small lamellulae; develops low crossveins beyond maturity, forking very rare; very light off-white, contrasting markedly with darker stem and cap. Stipe: 2–7 × 10–38 mm, cylindric, straight concolorous with cap, sparse white tomentum at base. Context: whitish, odor unremarkable.

Micromorphology: Basidiospores (128 spores, 5 sporocarps, 5 collections) 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 pleuro-, cheilo- or caulocystidia. Clamp connections in all tissues.

Habitat: Grows with mosses in grassland, fens, moors and bogs; usually 1–4 basidiomata in bogs, but troops of 20 or more in grassland. Season: June–Sept, most plentiful Jul–Aug. Found in the same bog at the same time as the other species.

Distribution: Throughout NL; North America and Europe.

Specimens examined: See Table 1.

Comments: Larger than the arrhenias, often reddish, not greyish, but otherwise similar to *Arr. philonotis*, but with narrower spores.

Dichotomous key to the species of sphagnicolous omphalinoids of 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 wooly, or may have adpressed scales, but not with raised scale tips) 4

3.a May undergo significant darkening reaction, spores $6.1\text{--}17.0 \times 3.0\text{--}6.1 \mu\text{m}$, ave. $10.3 \times 4.6 \mu\text{m}$
..... *Arrhenia bigelowii*

3b. No darkening reaction, spores $6.2\text{--}12.9 \times 2.8\text{--}5.6 \mu\text{m}$, ave. $8.9 \times 4.2 \mu\text{m}$ *Arrhenia gerardiana*.

4a. Medium (\pm reddish) brown, mature cap around 30 mm diameter, spores $<5 \mu\text{m}$ wide, distribution throughout NL
..... OPCUS

4b. Not as above 5

5a. Dark brown, nearly black, northerly distribution, obligate sphagnophile, spores $5.3\text{--}11.3 \times 3.3\text{--}6.6$, ave. 7.3×4.7
..... *Arrhenia telmatiaea*

5b. Medium to light grey-brown, northerly distribution, facultative sphagnophile, spores $6.6\text{--}10.9 \times 4.2\text{--}7.7$, ave. 8.7×5.6 *Arrhenia philonotis*

Discussion

Sphagnicolous omphalinoid arrhenias 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. Because we have a large number of collections from a wide geographic range (Table 3) the likelihood of finding additional sphagnicolous arrhenias 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 & 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 singletons identified as “*Arrhenia sphagnicola*”, which we excluded from the current study due to lack of photograph or detailed notes. After concluding our study, we encountered another singleton in *Sphagnum* that we were unable to identify or match to any known name (Voitk & Burzynski 2018). Extraction of DNA failed, so it was not incorporated into this study. We mention these collections to note that the possibility of finding additional sphagnicolous species in less commonly explored regions may not be exhausted.

Our molecular studies identified four species, confirming the impression expressed in the Introduction that few species were involved. Once clades were circumscribed phylogenetically, we could examine them retrospectively for identifying and differentiating characters. Thus, molecular studies provided the first opportunity to seek morphologic and ecologic characters that best match protologues and original material of available names. Before molecular studies, in the last seven decades leading students of these taxa used at least eight names for four species, so that no matter which names are used, accommodation and change will be required. Current uncertainty in the community is well illustrated 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. 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 the name has been applied to more than one species. Such lack of consistency means that any circumscription of species concepts will require significant change. In this situation, any system providing objective identification characters fixed to types would be welcome, with little convincing reason to prefer names other than those with the best fit to original material.

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 sphagnicolous 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. sphagnicola* with the rough scaliness of sphagnicolous 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 2021). 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 a darker specimen of *Arr. philonotis* (Fig. 5b), desquamated older *Arr. gerardiana* (Fig. 3d; 4f), or the unexpected OPCUS. In addition, the ill-understood darkening reaction, sometimes extreme (Fig. 4b, d), of *Arr. bigelowii* adds further confusion to these two taxa, compounded by the confusion over which is scaly and which is not.

Spore size is genetically determined, and functioned as a reliable 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. 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 & Lange (1982), who reported 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. Fig. 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 *philonotis* and *oniscus*, both used in eight studies. Both *Arr. telmatiaea* and *Arr. philonotis* are smooth-capped cold temperature species, far less common than their scaly-capped relatives. Their frequency in these studies probably reflects the habitats of interest to the workers more than the relative prevalence of the species. 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 Kuper (1995)

could also fit, but seem to fit better with *Arr. philinotis* 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*, but the frequency of its use among this small selection of workers does not tell the whole story. Figure 8 shows that epithets other than *oniscus* have also been applied to species with spores matching those of *Arr. telmatiaea*: *fusconigra* (Bon 1997, Cléménçon 1982; but not Bigelow 1985), *icmadophila* (Bigelow 1958, Redhead 1979), and *epichysium* (Lange & Lange 1982). In addition, Fig. 8g suggests that some collections called *philonotis* (Kuyper 1995, Lange & Lange 1982) may be or have had an admixture of *Arr. telmatiaea*.

Of course, spore measurements alone are insufficient for species circumscription. *Arrhenia telmatiaea* is an obligatory sphagnophile. Our observations in this regard agree with the illustration of the type by Masee 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. telmatiaea*, only one (Gminder 2001) described it as an obligatory sphagnophile. Five (Favre 1948, Cléménçon 1982, Bigelow 1985, Breitenbach & Kränzin 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, clearly some species other than *Arr. telmatiaea* must have also been considered part of the taxon to which *oniscus* had been applied. The most likely candidate is *Arr. philinotis*, which shares its darker colour, smooth cap, liking for moorland in cold climates, and a large overlap of spore size, but not the obligatory relationship to *Sphagnum*.

Thus, despite the seeming frequency of using *oniscus* among leading workers, uniform nomenclatural-taxonomic consistency is lacking even in this small sampling. Using spore size as the only criterion, the epithet may be applied to the same species seven times, and possibly applied to another species once, while up to four other epithets may have been applied to the same species as well. Such conclusion produces major conflict with the reported ecology of the same entity, and vice versa. Using additional criteria make things worse, not better. For example, as mentioned earlier, consideration of cap ornamentation and texture produces additional confusion. In the case of *Arr. telmatiaea* the matter is confused even more by its later synonym, *O. fusconigra*, a smooth-capped species often misinterpreted as scaly. This problem caused Bigelow (1985) to err by synonymizing his correctly identified new scaly-capped taxon with this smooth-capped one, despite the difference in spore size and shape.

Because a) this lack of taxonomic-nomenclatural consistency among leading workers will cause significant change in past practice no matter what name is fixed, b) nomenclatural study has revealed that *Ag. oniscus* is a later synonym for the current *L. umbellifera*, typified with that species (Voitk 2021), and c) there is available type material that fits the taxon without conflict, we elected to apply the earliest available sequence-confirmed name to this taxon. Selecting an optimal course becomes a matter of opinion. In our opinion, the extent of nomenclatural and taxonomic inconsistency argues against selecting any name shown to cause significant conflict with this group over *Ag. telmatiaeus*, whose sequenced type (along with the sequenced type of *O. fusconigra*) nestles in this clade. The name *Agaricus telmatiaeus* 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 & 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 incrustated pigmentation, was uncertain about its correct placement. Examination of our own collections confirms that the species has incrustated pigment in cap hyphae (Fig. 7d). Applying a name that produces conflict with the original material is likely to become a potential focus for repeated future attempts at rectification. Should other workers consider a more frequently used epithet more advantageous, the Code provides a mechanism to conserve one name over another. Such legitimate conservation of a name over an optimally fitting one, via rules in place to serve the best interests of the users, should eliminate future temptation to change nomenclature far better than arbitrary selection of a name causing conflict at this time.

Similar inconsistency was observed with the three other species. Epithets with spore measurements fitting best with *Arr. philonotis* were *philonotis* (Favre 1948; Clémenton 1982; Bon 1997, Elborne 2008) and *umbratilis* (Lange & Lange 1982). Bon described the species as an obligatory sphagniphile, 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; Clémenton 1982; Breitelbach & Kränzlin 1991; Bon 1997), and *fusca* (Bigelow 1958).

In other words, past nomenclature has been inconsistent even in the hands of 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 some degree of instability in this small group of taxa.

In addition to the three obligate sphagnophiles, we identified *Arr. philonotis* as a facultative sphagnophile. Whether it interacts with *Sphagnum*, or merely shares with it a like for similar habitats is a matter for investigation. 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 *Ag. philonotis*, presumed lost, came from a bog close to Berlin, near the North Sea. The closest collection with good material that we sequenced came from a bog near Baden-Württemberg, Germany, a more midcontinental location in the foothills of the Alps, about 500 m asl. Although the biome differs slightly, 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.

Finally, finding OPCUS, a facultative sphagnicolous species of *Omphalina*, was a pleasant surprise. Our study is focused on sphagnicolous arrhenias, but because OPCUS can be confused with them with ease, we present an informal description to alert the reader. Based on sequence studies to date, this is the only species of *Omphalina* in the NL. If there is a relationship with sphagnum, it is facultative, because the same species was encountered much more frequently in low-moss boreal grasslands on poor soil. Despite the reputed reddish colouration of omphalinas, macroscopic morphology was not always enough to separate some specimens of OPCUS (Fig. 5f, g) from *Arr. philonotis* (Fig. 3e; 5a, b), a non-blackish *Arr. telmatiaea* (Fig. 3f) or particularly from the more similar desquamated older *Arr. gerardiana* (Fig. 3d; 4f), a species that can appear reddish at times. However, OPCUS can be separated from these readily by spore size. Phylogenetic type studies of the *Omphalina pyxidata* complex to identify OPCUS, are outside the scope of the present study, but have been taken up by a colleague.

This experience demonstrates the major contribution of molecular analysis to taxonomy. When we rank organisms, we use their characters to separate them. 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. Using molecular analysis to circumscribe the species in a group, permits 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, which should bring about lasting stability to this relatively small group of interesting fungi.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

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

Availability of data and materials

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

Competing interests

The authors have no relevant financial or other competing interests to disclose.

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Authors' contributions

AV and EL were primary contributors to study conception and design. Material preparation, data collection and analysis were performed by all authors. The first draft of the manuscript was written by AV and all authors commented on it and subsequent versions of the manuscript. All authors read and approved the final manuscript.

Code availability Not applicable.

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Figures

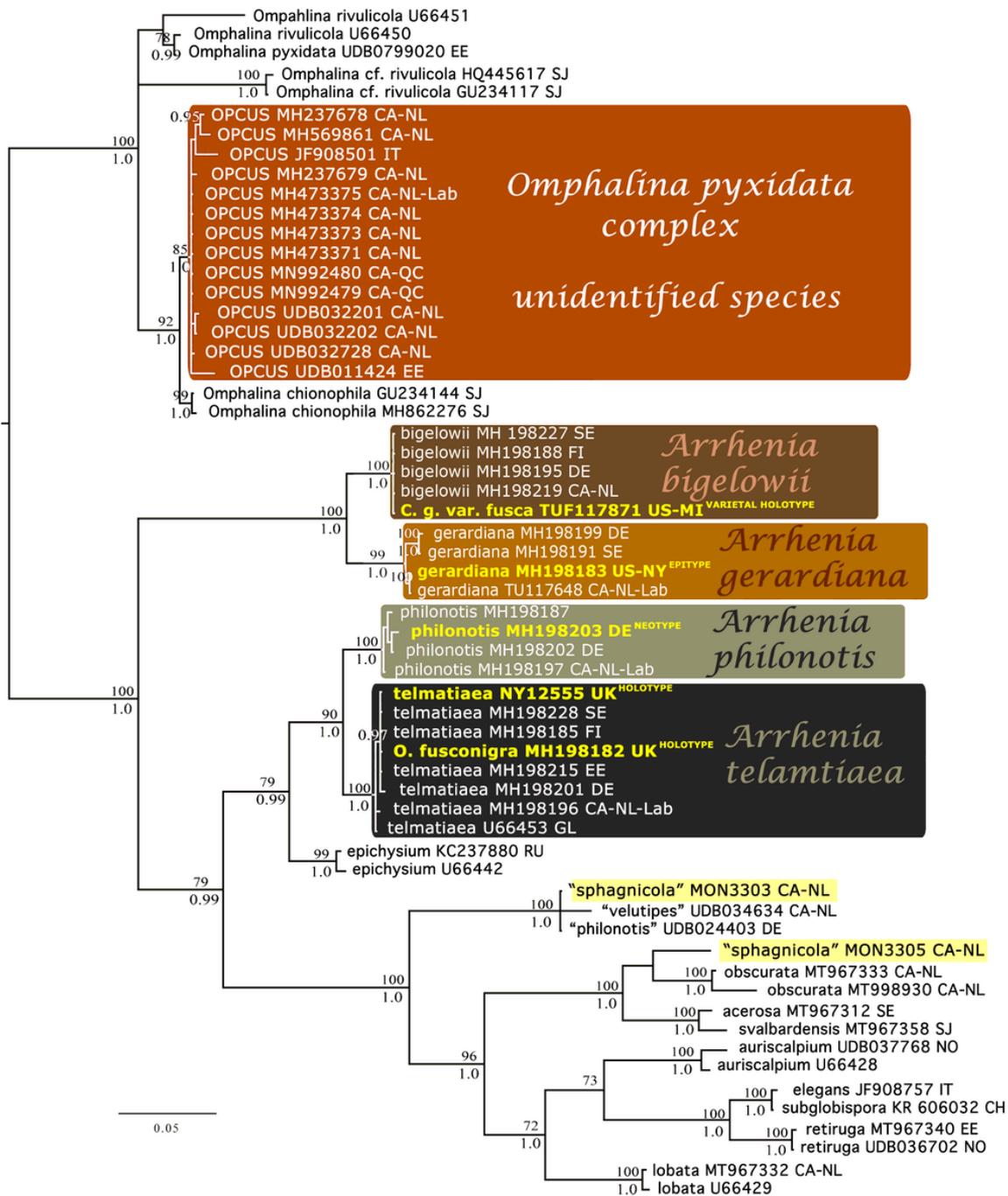


Figure 1

Placement of the sphagnicolous arrhenias within *Arrhenia*, and OPCUS (as “*Omphalina cf. pyxidata*”) within *Omphalina*. Note the unidentified singletons, “*sphagnicola*”, collected as presumptive sphagnicolous arrhenias, but not treated here due to lack of data. ML bootstrap support $\geq 70\%$ and the Bayesian posterior probabilities $\geq 95\%$ are shown above and below the branches (bs/pp), respectively

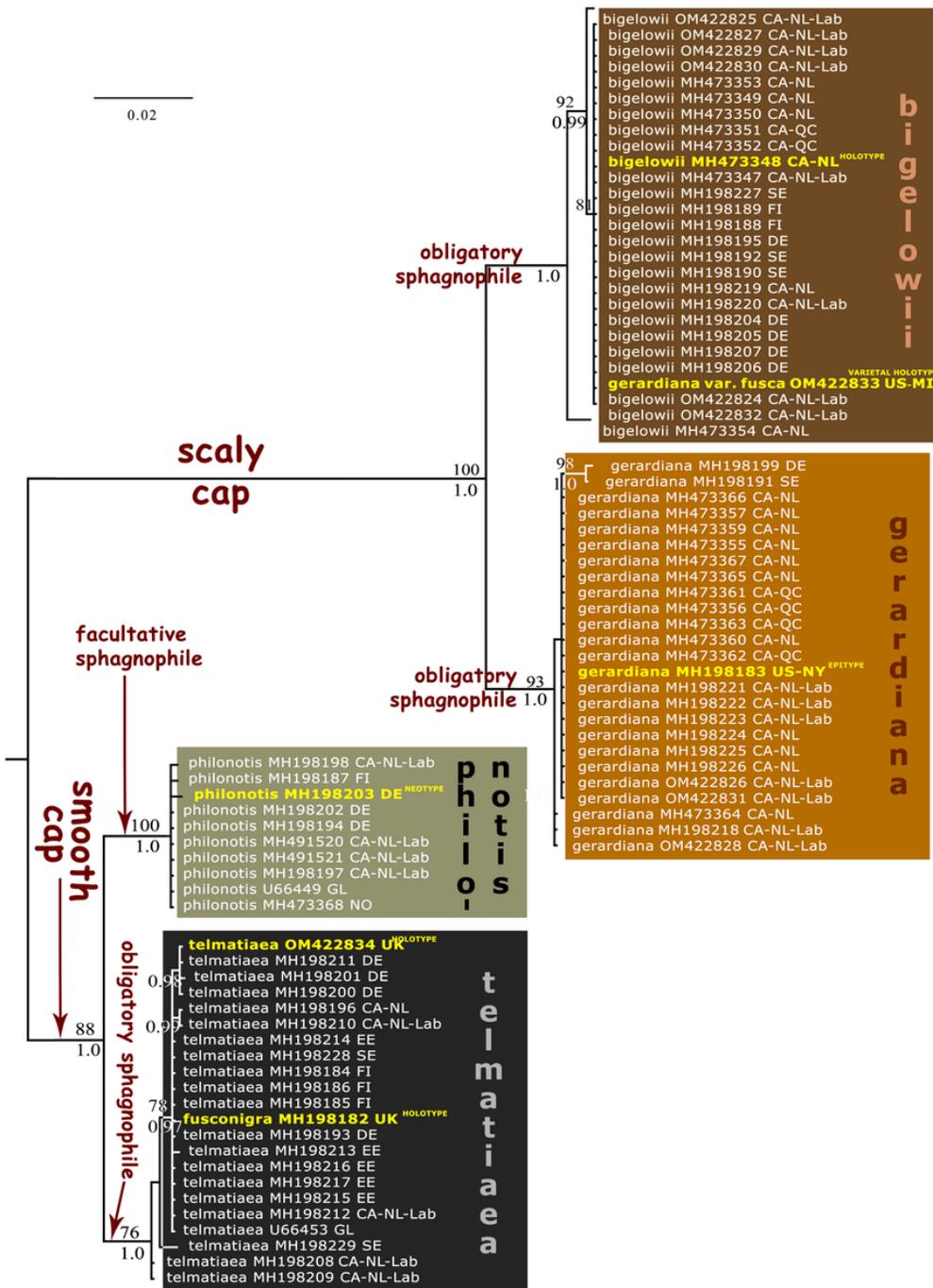


Figure 2

Best-scoring tree focusing on the four formally accepted sphagnicolous arhenias, based on maximum likelihood analysis of the ITS barcoding marker. Country (plus province/state for US and CA) identified by ISO Alpha 2 codes. "Lab" marks NL specimens from Labrador. Types shown in bold yellow. Specimens identified by current names, except types, identified by the original epithets. All sequences were generated for this study, except U66449 and U66453, the only deposits in GenBank from this group when we began this investigation. ML bootstrap support $\geq 70\%$ and the Bayesian posterior probabilities $\geq 95\%$ are shown above and below the branches (bs/pp), respectively

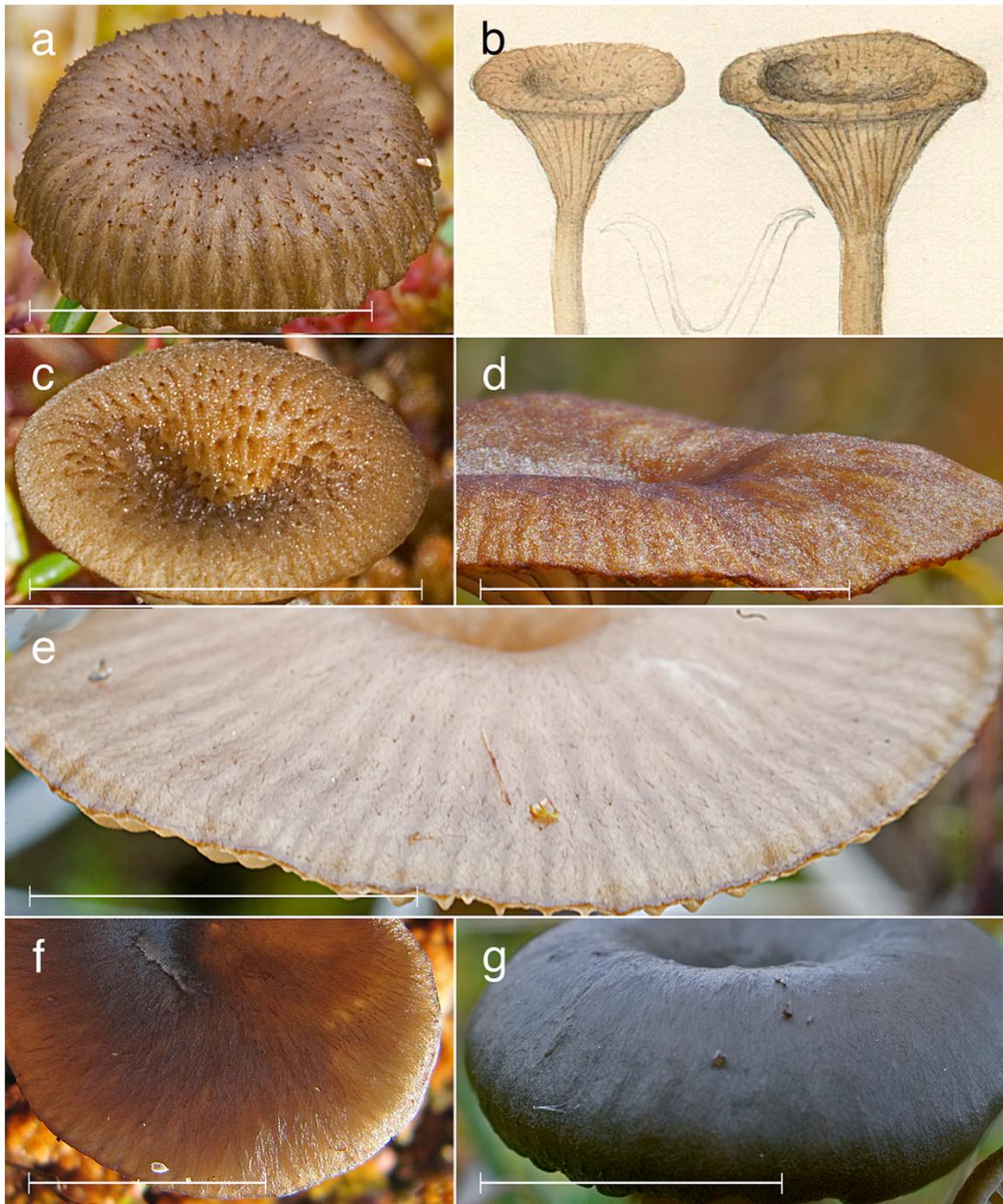


Figure 3

Cap texture of sphagnicolous arrhenias. Bars = 10 mm. **a.** The dramatically scaly cap of *Arr. bigelowii* (08.08.12.av05), unlikely to be described by diminutives, “sparsely woolly” or “minutely squamulose”. **b.** Peck’s aquarelle of his *Ag. gerardianus* 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 addressed in the pileipellis, with no attempts of the tips to rise. **g.** Cap of a very dark *Arr. telmatiaea* (05.09.08.av02). The addressed “scale pattern” in the pileipellis is present, although not as evident

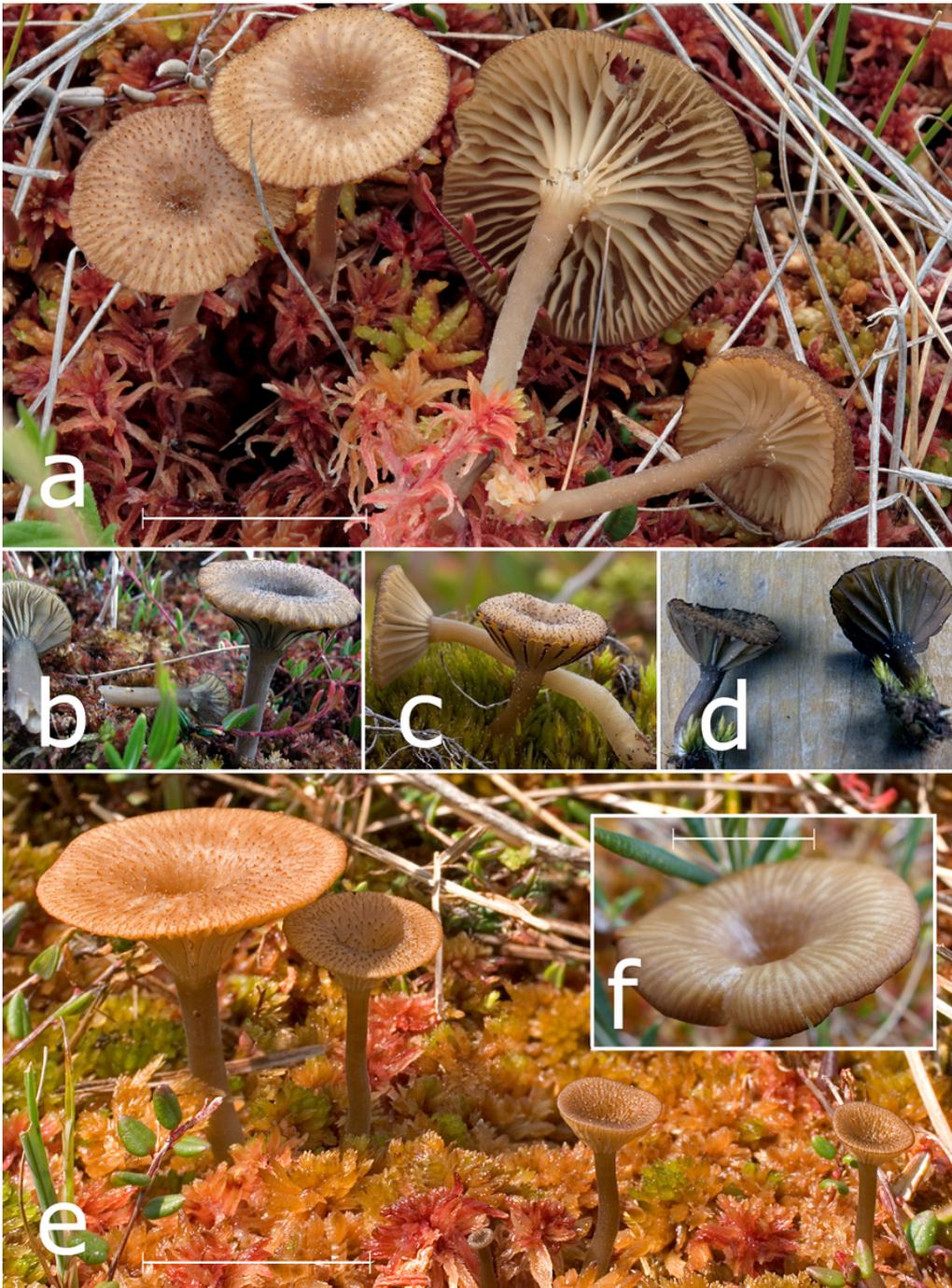


Figure 4

Scaly-capped sphagnicolous 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.** Collection 05.06.15.av01: in situ appearance at the time of collection. **d.** Appearance when taken from collecting basket, ca. 3 hours 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 specimen (17.07.04.av02) with scales no longer evident (see also Fig. 3d)

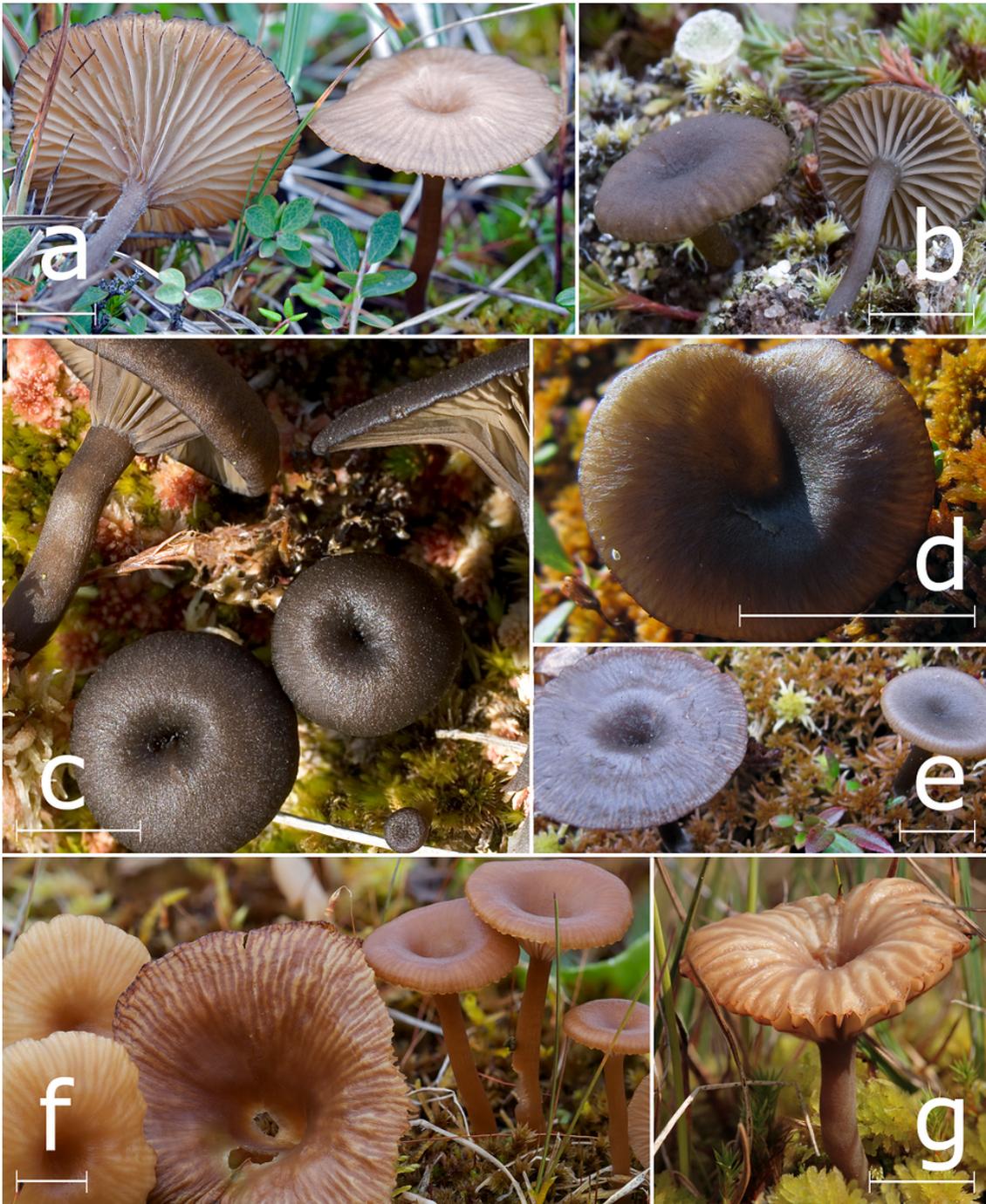


Figure 5

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.** OPCUS (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.** OPCUS (07.07.24.av01) growing in *Sphagnum*

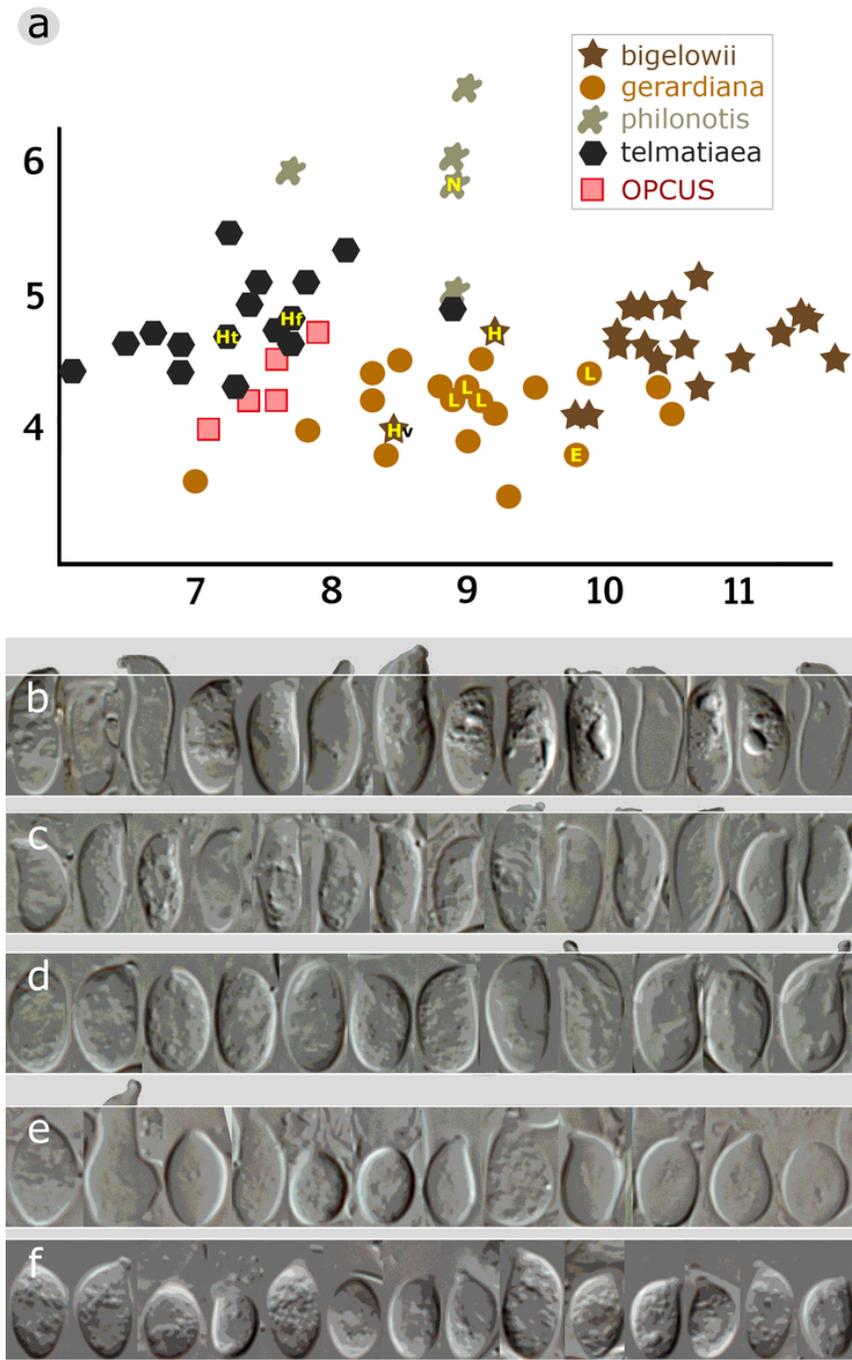


Figure 6

Basidiospores of studied species. **a**. Average spore sizes of sequence-identified sphagnicolous omphalinoids, length in μm on x-axis, width on y-axis. H = holotype; Hv = varietal holotype; Ht = holotype of *Ag. telmatiaeus*, Hf = holotype of *O. fusconigra*; N = neotype; L = lectotype (4 basiomata, not sequenced); E = epitype. **b–f**. basidiospores of the studied species. Upper white line marks $10\ \mu\text{m}$. **b**. *Arr. bigelowii*, **c**. *Arr. gerardiana*, **d**. *Arr. philonotis*, **e**. *Arr. telmatiaea*, **f**. OPCUS.

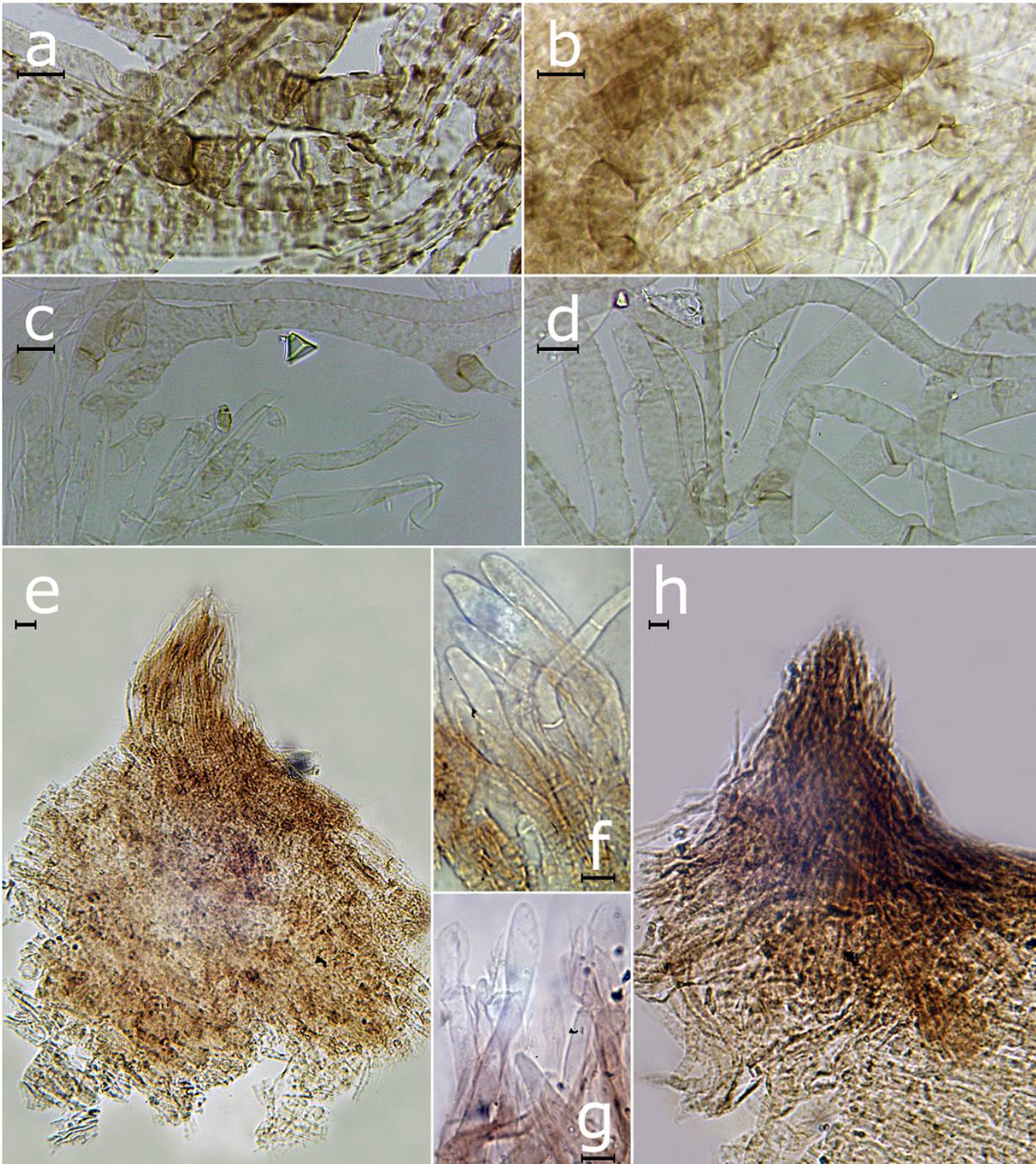


Figure 7

Cap micromorphology. Scale bars 10 μm . **a.** Incrusting pigment *Arr. bigelowii* (08.08.12.av05). **b.** Incrusting pigment *Arr. gerardiana* (17.07.05.av05). **c.** Incrusting pigment *Arr. philonoitis* (KL-015). **d.** Incrusting 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.** Scales of *Arr. gerardiana* (10.07.13.av06)

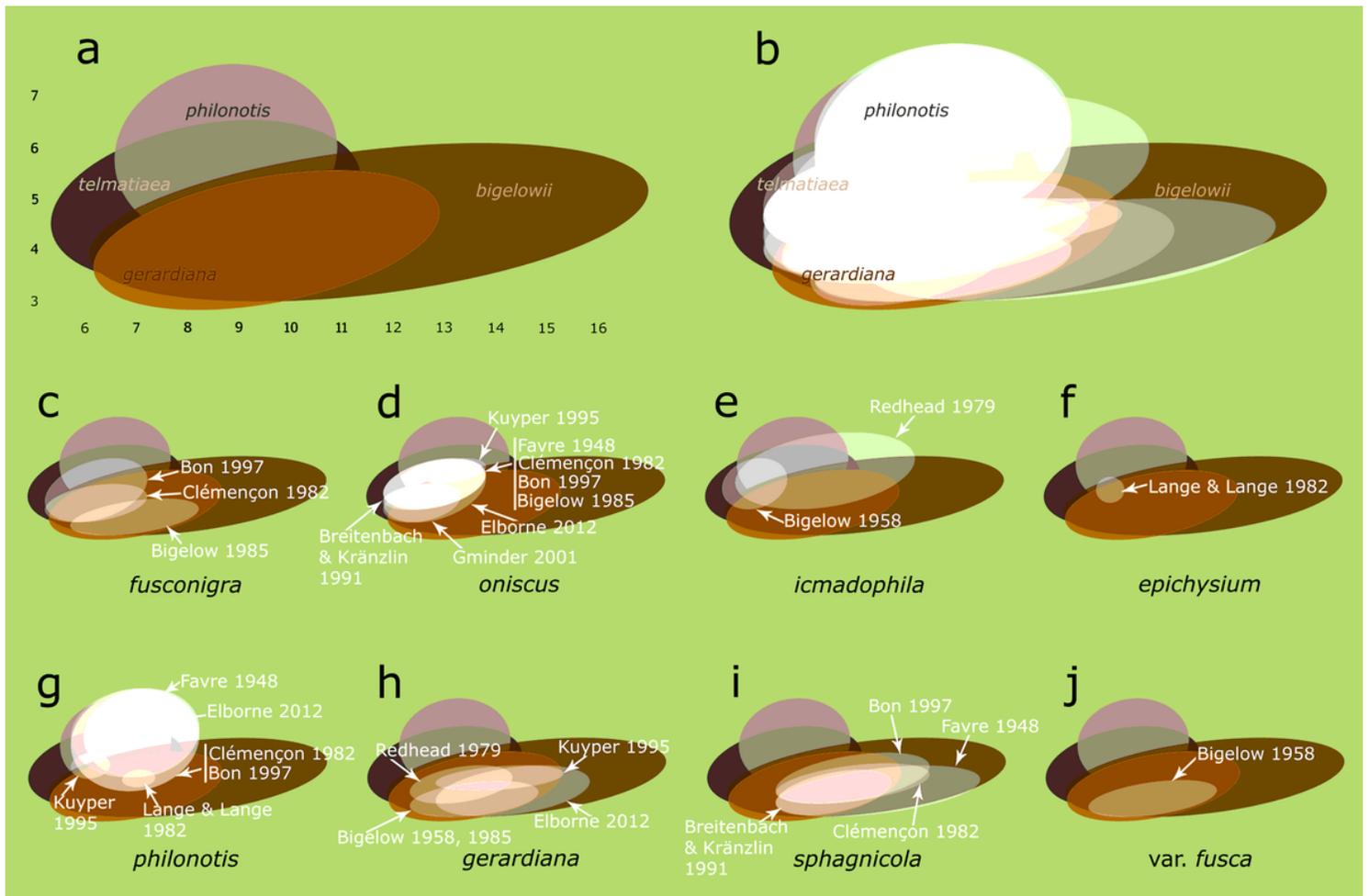


Figure 8

Comparison of spore measurements of our four species, with those reported in the ten major publications cited in the Introduction. **a.** Measurement as for Fig. 6. Ranges for our four species. **b.** Combined ranges of all species reported by all cited authors, represented by translucent white ovals superimposed on our results. **c–j.** Ranges for each epithet used by the cited authors on each separate view, again superimposed on our measurements. The ranges recorded by Lange & Lange (1982) are for average values of the collections, not the complete range.